M LIBRARY

JAN 10 1949

Volume 22 NOVEMBER, 1948 Number 6

JOURNAL OF PALEONTOLOGY

A publication of The Society of Economic Paleontologists and Mineralogists *and* The Paleontological Society *with the generous support and cooperation of* The American Association of Petroleum Geologists *and* The Geological Society of America

CONTENTS

The cephalopod fauna of the Mississippian Barnett formation of central Texas ..... *A. K. Miller and Walter Youngquist* 649

A cephalopod fauna from the type section of the Pennsylvanian "Winslow Formation" of Arkansas ..... *A. K. Miller and R. H. Downs* 672

Pteridosperm male fructifications: American species of *Dolerotheca*, with notes regarding certain allied forms ..... *James M. Schopf* 681

Studies in quantitative paleontology: I. Some aspects of the theory and practice of quantitative invertebrate paleontology ..... *Benjamin H. Burma* 725

Eocene algae from Florida ..... *J. Harlan Johnson and Bernard J. Ferris* 762

Some Pennsylvanian conodonts from Iowa .. *Walter Youngquist and Bruce C. Heezen* 767

Foramanifera from the Miocene Astoria formation in southwestern Washington .... *Weldon W. Rau* 774

Molluscan faunule from Devonian Island Mesa beds, Arizona .... *Alexander Stoyanow* 783

The ostracode genus *Cythereis* ..... *P. C. Sylvester-Bradley* 792

Upper Cambrian trilobites from Oklahoma ..... *E. A. Frederickson* 798

A new *Pecten* from the upper Miocene of California ..... *U. S. Grant and Robert E. Stevenson* 804

ERRATA 806

INDEX 807

EDITORS

A Scott Warthin, for The Paleontological Society.

J. Marvin Weller, for The Society of Economic Paleontologists and Mineralogists.

The Journal of Paleontology is published bi-monthly. The numbers issued in January, May, and September are sponsored by The Paleontological Society in cooperation with The Geological Society of America; those issued in March, July, and November are sponsored by The Society of Economic Paleontologists and Mineralogists in cooperation with The American Association of Petroleum Geologists.

The subscription price of the Journal of Paleontology is $6.00 per year prepaid to addresses in the United States.

Single numbers, $2.00 each.

Postage is charged extra for all other countries in the Postal Union, 40 cents on annual subscriptions (total $6.40).

The Journal will furnish reprints at cost. Orders should accompany manuscript.

Communications about the Journal, subscriptions, rates, memberships, change of address, and nonreceipt of preceding numbers should be addressed to Society of Economic Paleontologists and Mineralogists, P. O. Box 979, Tulsa 1, Oklahoma. Claims for nonreceipt of preceding numbers must be sent in within three months of the date of publication in order to be filled gratis. Communications in regard to advertising should be addressed to J. Marvin Weller, Walker Museum, University of Chicago, Chicago 37, Ill.

Communications in regard to manuscripts or purely editorial matters should be addressed to J. Marvin Weller, Walker Museum, University of Chicago, Chicago 37, Ill. or to A. Scott Warthin, Vassar College, Poughkeepsie, N.Y.

Contributors are requested to instruct their photographers to illuminate fossils from the upper left side, the conventional manner. Plates normally should be arranged for publication at the size of 5¼ by 7⅛ inches, exclusive of margins, heading, and title. Printed numerals of standard size and form may be obtained free from either editor. When requesting them state number of plates and the dimensions of each plate.

Entered as second-class matter at the Post Office at Tulsa 1, Oklahoma, under the Act of March 3, 1879. Acceptance for mailing at special rate of postage provided for in paragraph 4, section 538, P. L. and R., authorized April 3, 1935.

Additional entry as second-class matter at the Post Office at Menasha, Wis.

GEORGE BANTA PUBLISHING COMPANY, MENASHA, WIS.

JOURNAL OF PALEONTOLOGY

A publication of THE SOCIETY OF ECONOMIC PALEONTOLOGISTS AND MINERALOGISTS *and* THE PALEONTOLOGICAL SOCIETY *with the generous support and cooperation of* THE AMERICAN ASSOCIATION OF PETROLEUM GEOLOGISTS *and* THE GEOLOGICAL SOCIETY OF AMERICA

VOLUME 22 NOVEMBER, 1948 NUMBER 6

THE CEPHALOPOD FAUNA OF THE MISSISSIPPIAN BARNETT FORMATION OF CENTRAL TEXAS

A. K. MILLER AND WALTER YOUNGQUIST

State University of Iowa, Iowa City, Iowa and University of Idaho, Moscow, Idaho

ABSTRACT—Nautiloids are rare in the Barnett formation, but representatives of the following genera are illustrated and described from it: *Mooreoceras*, *Poterioceras?*, *Endolobus*, and *Discitoceras*. Locally six genera of ammonoids are relatively abundant in the same formation: *Cravenoceras*, *Goniatites*, *Lyrogoniatites*, *Neoglyphioceras*, *Eumorphoceras*, and *Girtyoceras*. The fauna of the Barnett is very much like that of the Helms formation of west Texas, the White Pine shale of Nevada and California, the Caney shale of Oklahoma, the "Meramec" of Kentucky, and the Moorefield, Ruddell, Batesville, and Fayetteville formations of Arkansas. The description of a representative of *Cravenoceras* from the Upper Mississippian Pitkin limestone of northern Arkansas is included as an appendix.

INTRODUCTION

THE Barnett formation, as now interpreted, is of rather widespread occurrence in central Texas. In the vicinity of the type section, near San Saba, it consists of some 40 to 50 feet of shale with limestone lenses and with a small amount of interbedded limestone in its upper portion. However, to the south and west it grades into detrital limestone with a thickness of as much as 140 feet, and to the north it has been found to be 100–200 feet thick in subsurface sections. Stratigraphically it lies disconformably between the early Mississippian Chappel limestone below and the Lower Pennsylvanian Marble Falls limestone above.

As long ago as 1861, Gabb described a single ammonoid from strata that are now regarded as part of the Barnett. He coined the name *Goniatites* [*Lyrogoniatites?*] *entogonus*[1] for this specimen, which came from 5 miles west of Lampasas, Texas.

In 1893 Hyatt published a study of a few additional specimens from the same general locality. One of these he referred with question to Gabb's species, and for the others he proposed the name *Glyphioceras cumminsi* [=*Goniatites choctawensis cumminsi* of the present report]. Hyatt also reported on some specimens from the same

[1] This species is now placed in *Lyrogoniatites*, largely because Hyatt (1893, pp. 472–473, pl. 47, figs. 49–51) referred to it with question a representative of that genus from the same locality. Although we are continuing this procedure, we recognize that from Gabb's description (which is not accompanied by an illustration) it is not possible to determine the generic affinities of his holotype, and that specimen may well be quite distinct from the individual Hyatt figured and described as probably conspecific. Clearly Gabb's specimen needs to be restudied, if it can be found.

formation near Richland Springs in San Saba County, and he termed them *Glyphioceras incisum* [=*Goniatites choctawensis* of the present report].

In his classical monograph of "The Carboniferous ammonoids of America," published in 1903, Smith reviewed all of the ammonoids known from the Barnett at that time. He referred them to three species which he called *Goniatites crenistria* Phillips, *G. striatus* Sowerby, and *Gastrioceras entogonum* (Gabb)—the first two of these species were originally based on British specimens. Earlier workers, like Gabb and Hyatt, merely referred to the beds from which their specimens came as "Carboniferous," but Smith recognized that the ammonoids are indicative of the Mississippian; he placed them (together with a few specimens from the Bend) in the "St. Louis-Chester," which he regarded as directly equivalent to the "Ste. Genevieve."

Some years later, Girty (1919, p. 71) pointed out that the Bend, as then defined, "is divided by an important unconformity and that the lower part is of Mississippian while the upper part is of Pennsylvanian age." In 1922 Plummer and Moore (p. 24) proposed separating the "Lower Bend shale" as an independent formation under the name Barnett shale, and they stated that it would be best "tentatively to retain this basal shale as a part of the Bend group," which they placed in the Lower Pennsylvanian. These authors discussed the ammonoids of the Barnett at some length and apparently concluded that none of them are referable to what they term "Old World species" for they (p. 29) state: "The cephalopods of the Barnett shale are without doubt an important element in the fauna which have a significant bearing on the age and correlation of the formation. Of these, four species are at present recognized: *Glyphioceras cumminsi*, *G. incisum*, a new species of *Glyphioceras*[2] and *Gastrioceras entogonum*." Girty (1926, pp. 3–4) noted that the Barnett contains "goniatites closely allied to the European species *G. crenistria* and *G. striatus*," and he emphasized that its fauna is "related to faunas of Mississippian age and only to faunas of Mississippian age." Furthermore, he pointed out that the "fauna of the Barnett shale would tend to link that formation with the lower part of the Caney shale, and . . . with the Moorefield shale"; but he was careful to add that "the lower Caney may represent the whole Moorefield-Fayetteville interval of the Arkansas section," and he believed that the Fayetteville was "definitely" Chester.

In their comprehensive report on the "Upper Paleozoic ammonites in Texas," Plummer and Scott (1937, pp. 14–15) state:

> The lowest ammonoid zone in the north-central Texas section is the *Neoglyphioceras newsomi* zone. This zone occurs at the base of the Barnett shale along the outcrop in San Saba and Lampasas counties, central Texas. This zone is of upper Mississippian age and corresponds to the *Neoglyphioceras caneyanum* zone of eastern Oklahoma and Arkansas and to the *Neoglyphioceras spirale* zone in Europe. The following ammonites occur in it:
>
> *Neoglyphioceras newsomi* (Smith)
> *Neoglyphioceras* [*Lyrogoniatites?*] *entogonum* (Gabb)
> *Neoglyphioceras caneyanum* (Girty)
> *Goniatites choctawensis* Shumard
> *Adelphoceras* [*Girtyoceras*] *meslerianum* Girty
>
> The second ammonoid zone is the *Eumorphoceras bisulcatum* zone. This occurs in a thin layer of limestone in the Barnett shale below the Marble Falls limestone. This zone is also of upper Mississippian age. . . . The following ammonoids have been collected from it:
>
> *Cravenoceras richardsonianum* (Girty) [=? *C. nevadense* of the present report]
> *Goniatites choctawensis* Shumard
> *Nuculoceras barnettense*, n. sp. [of Plummer and Scott] [=? *C. hesperium* and/or *C. nevadense* of the present report]
> *Nuculoceras incisum* (Hyatt) [=? *C. hesperium* and/or *C. nevadense* of the present report]
> *Eumorphoceras bisulcatum* Girty
> *Welleriles mohri*, n. sp. [of Plummer and Scott[3]].

Very recently, Cloud and Barnes (Manuscript in press) have discussed the Barnett shale and its fauna at some length. They conclude that the

> lower limit of its age is virtually fixed as Keokuk, but the upper limit may be as high as Ste. Genevieve. The present authors [Cloud and Barnes] consider it extremely unlikely that any part of the Barnett formation is as young as Chester in

[2] This form was placed in synonymy with *Glyphioceras incisum* Hyatt by Plummer and Scott in 1937 (p. 106).

[3] These authors (1938, p. 1920) have since indicated that this species occurs in the Pennsylvanian Millsap Lake formation rather than in the Barnett shale.

age, and they are inclined to suspect that detailed biostratigraphic studies will prove it to be entirely pre-St. Louis. The greater number of species from the middle Mississippi Valley region that compare closely with Barnett species are either restricted to the Keokuk limestone or are known to occur in it. It is possible, therefore, that the Barnett formation and its correlatives are wholly of Keokuk age.

Cloud and Barnes, together with G. A. Cooper, collected several hundred cephalopods from the Barnett, which they made available to us for study. These specimens constitute the primary basis for the present report. They show that, as had been mentioned by Plummer and Scott, and by Cloud and Barnes, the genus *Goniatites s. s.* occurs in the Barnett in direct association with *Eumorphoceras bisulcatum*. Girty (1909, p. 10; 1918, p. 39) had already indicated that these two forms probably occur together in the Caney shale of Oklahoma and the White Pine shale of California. However, in Europe, where Middle Carboniferous ammonoid zones have been given careful consideration, the genus *Goniatites s. s.* is said to be represented only in the Viséan, and *Eumorphoceras* is stated to be limited to the next higher zone, that is, to the lower Namurian. Therefore, Miller and Furnish (1940, p. 357) concluded that the Caney, Barnett, and related formations contain two ammonoid zones, one of which is about Meramec in age whereas the other is Chester. The collections now available for study indicate that there is only one faunal zone in the Barnett, but we are not able to ascertain with certainty whether the fauna is upper Viséan or lower Namurian (or both) in age. Furthermore, the cephalopods do not indicate the correlative of the Barnett in the classical Mississippian section of the middle Mississippi Valley, for the beds there have yielded too few ammonoids. However, from a study of the cephalopods alone, we can conclude that the Barnett is of approximately the same age as the Caney of Oklahoma, the Moorefield, Ruddell, Batesville, and/or lower Fayetteville of Arkansas, the "Meramec" of Kentucky, the Helms of west Texas, the White Pine of Nevada and southeastern California, and the goniatite-bearing portions of the Floyd of Georgia.

In the present state of our knowledge, it seems that the most nearly complete American sequence of ammonoid-bearing beds of this general age is in Arkansas. The Moorefield, Ruddell, Batesville, Fayetteville, and Pitkin there have all yielded ammonoids. The specimens in them are, however, not as well preserved or abundant as are those in the Caney and the Barnett. Nevertheless, these formations seem to offer the best possibility of determining the stratigraphic ranges in America of the various ammonoid genera under consideration.

The photographs which accompany this study were retouched by Mr. Howard E. Webster, who also prepared the text figures. The completion of the report was made financially possible by the Graduate College of the State University of Iowa. Dr. Preston E. Cloud, Jr., read the entire manuscript and made many helpful suggestions.

COLLECTING LOCALITIES

Most of the specimens we have studied came from two localities in central Texas, and the others are from three additional localities in the same general region. In the following paragraphs each of these localities is described in detail and the cephalopods known from it are listed.

The most prolific locality is in southwestern Mason County, in the "Bear Spring area" of Cloud and Barnes—their locality TF-422. The specimens came from about 5000 feet N. 54°W. from the point where the county road from Mason to White's Crossing crosses Honey Creek, which itself is about 8 miles by road southwest of Mason. Here the Barnett is some 90 feet thick. The basal 30 feet is white fine- to medium-grained crinoidal limestone, whereas the upper beds include petroliferous limestone and shale interbedded with coarse crinoidal limestone. The cephalopods, which occur here in association with many other fossils, came from beds estimated to be between 5 and 15 feet below the Barnett-Marble Falls contact, and they consist of the following species:

Mooreoceras crebriliratum (Girty)
Posterioceras? sp.
Endolobus sp.
Discitoceras texanum Miller and Youngquist, n. sp.
Cravenoceras hesperium Miller and Furnish?

Cravenoceras nevadense Miller and Furnish
Cravenoceras scotti Miller and Youngquist, n. sp.
Goniatites choctawensis Shumard
Eumorphoceras bisulcatum Girty
Eumorphoceras plummeri Miller and Youngquist, n. sp.
Girtyoceras meslerianum (Girty)

The other locality which yielded numerous specimens is an "exposure of shale beds and thin limestone near top of hill and east of old lime kiln, [2½ or] 3 miles southeast of San Saba on Chappel road," San Saba County [Univ. Texas locality 205-T-24, see Plummer and Scott, 1937, p. 409]. Plummer and Scott described four species of ammonoids from this locality, and altogether the following forms are now known from it:

Cravenoceras nevadense Miller and Furnish
Goniatites choctawensis Shumard
Lyrogoniatites cloudi Miller and Youngquist, n. sp.
Lyrogoniatites? entogonus (Gabb)
Neoglyphioceras caneyanum (Girty) [*fide* Plummer and Scott]
Neoglyphioceras newsomi (Smith) [*fide* Plummer and Scott]
Eumorphoceras bisulcatum Girty
Eumorphoceras plummeri Miller and Youngquist, n. sp.
Girtyoceras meslerianum (Girty)
Girtyoceras ornatissimum Miller and Youngquist, n. sp.

We have a few specimens from a second locality (TF-418 of Cloud and Barnes) in the "Bear Spring area" of southwestern Mason County. They came from about 3100 to 3200 feet S. 14°W. of the southwest end of the concrete pavement at White's Crossing of Llano River, which is about 10 miles by road southwest of Mason. The fossils occur there in a 140-foot section of white crinoidal limesands of the Barnett formation on the northwest slope, and near the southwest end of an elongate hill south of Bee Branch. Specimens of *Cravenoceras nevadense* Miller and Furnish and *Goniatites choctawensis* Shumard were collected about 20 feet above the contact of the limesands of the Barnett with the underlying Chappel limestone, in association with pelecypods and *Pleurodictyum* [and (*fide* Cloud and Barnes) 2 feet above a bed containing *Spirifer logani* Hall, *Leptaena* cf. *L. analoga* (Phillips), and at least five other genera and species of brachiopods; and 1 foot above a bed containing *Orthotetes* aff. *O. keokuk* (Hall) and at least 11 other species]. Both species were also secured about 72 feet above this zone and 92 feet above the base of the Barnett; this is about 48 feet below the Barnett-Marble Falls contact and 18 feet below the highest bed in which *Orthotetes* aff. *O. keokuk* (Hall) was found by Cloud and Barnes.

A few specimens were collected in southeastern Llano County, in Cloud and Barnes' "Moore Hollow area"—their locality TF-429. This place is 1900 feet due west from a point 1.93 miles south of the Honey Creek crossing of the Llano-Click road, which is about 15 miles by road southeast of Llano. The Barnett is only about 10 feet thick here and the fossils were obtained from a block of limestone float which almost certainly came from near the very top of the formation. This locality has yielded *Cravenoceras hesperium* Miller and Furnish?, *C. nevadense* Miller and Furnish, *Goniatites choctawensis* Shumard, and *Eumorphoceras bisulcatum* Girty.

John Emery Adams sent us a few ammonoids from near the top of the Barnett shale along the San Saba-Bend road about 7 miles east of San Saba. These represent *Cravenoceras nevadense* Miller and Furnish?,

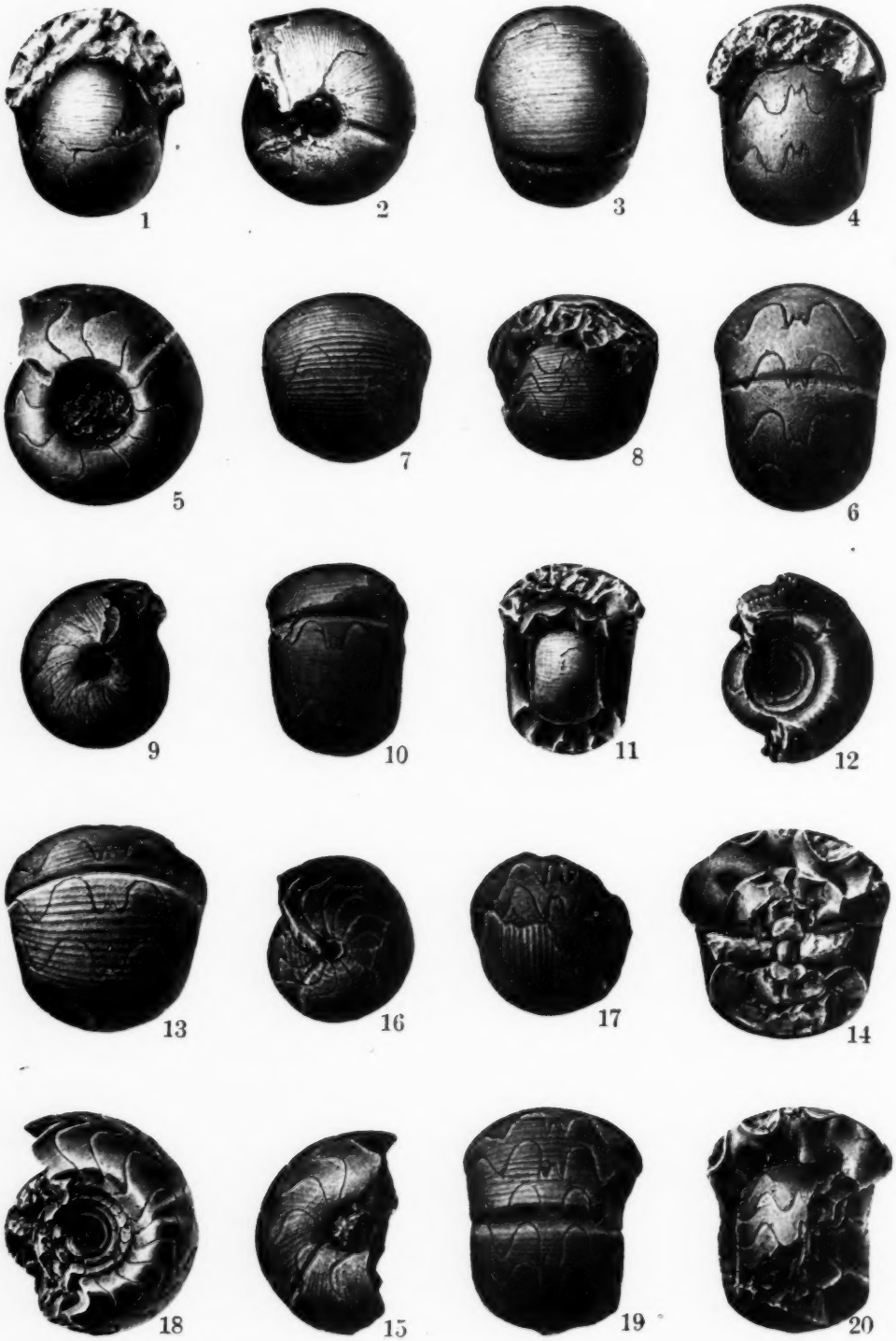
---

EXPLANATION OF PLATE 94

All specimens, except those illustrated by figures *1–3*, are from the upper part of the Barnett shale about 8 miles southwest of Mason, Texas. The specimen represented by figures *1–3* came from the same formation about 2½ miles south-southeast of San Saba, Texas.

FIGS. *1–3*—*Lyrogoniatites cloudi*, n. sp. The holotype ×1½. (p. 660)
4, 5—*Mooreceras crebriliratum* (Girty). Two specimens, ×1½. (p. 653)
6—*Discitoceras texanum*, n. sp. The holotype, ×1½ (p. 654)
7, 8—*Endolobus* sp. Part of a phragmacone, ×1. (p. 654)
9—*Posterioceras?* sp. ×1½. (p. 653)
10, 11—*Girtyoceras meslerianum* (Girty). A large completely septate specimen, ×1. (p. 667)

Miller and Youngquist, Mississippian Cephalopoda



Miller and Youngquist, Mississippian Cephalopoda

Eumorphoceras bisulcatum Girty, and *E. Plummeri*, n. sp.

Altogether, the following cephalopod species, as identified by us, are now known from the Barnett formation:

Mooreoceras crebriliratum (Girty)
Poterioceras? sp.
Endolobus sp.
Discitoceras texanum Miller and Youngquist, n. sp.
Cravenoceras hesperium Miller and Furnish?
Cravenoceras nevadense Miller and Furnish
Cravenoceras scotti Miller and Youngquist, n. sp.
Goniatites choctawensis Girty
Lyrogoniatites? entogonus (Gabb)
Lyrogoniatites cloudi Miller and Youngquist, n. sp.
Neoglyphioceras caneyanum (Girty) [*fide* Plummer and Scott]
Neoglyphioceras newsomi (Smith) [*fide* Plummer and Scott]
Eumorphoceras bisulcatum Girty
Eumorphoceras plummeri Miller and Youngquist, n. sp.
Girtyoceras meslerianum (Girty)
Girtyoceras ornatissimum Miller and Youngquist, n. sp.

SYSTEMATIC PALEONTOLOGY

MOOREOCERAS CREBRILIRATUM (Girty)
Plate 94, figures 4, 5

Orthoceras crebriliratum GIRTY, 1909, U. S. Geol. Survey Bull. 377, pp. 9, 46, pl. 6, figs. 9–10; ?GORDON, 1944, Am. Assoc. Petroleum Geol., Bull., vol. 28, p. 1630.

Our collections contain a few fragmentary orthoceracones, two of which are figured. In these, the conch is circular in cross section and very gradually expanded orad. The test is moderately thick, and it bears numerous fine lirae that are essentially straight and directly transverse. There are about two and one-half camerae in a length equal to the diameter of the conch. The sutures form simple circles as they are straight and transverse to the long axis of the conch. At least at its passage through the septa, the siphuncle is small and almost (but not quite) central in position. At the adapical end of the larger of the figured specimens, the diameter of the conch is about 10 mm. and that of the siphuncle about 1 mm.

Remarks.—These specimens seem to resemble the syntypes in all available particulars. Most of the type specimens are small, but one of them is stated to have a diameter of 15 mm., which is greater than that of our largest specimen.

Occurrence.—Upper part of Barnett formation about 5000 feet N. 54°W. from the point where the county road from Mason to White's Crossing crosses Honey Creek, which itself is about 8 miles by road southwest of Mason, Mason County, Texas. The syntypes came from the Caney shale of southeastern Oklahoma, and a closely related or identical form occurs in the Moorefield shale of northern Arkansas.

Repository.—U. S. National Museum.

POTERIOCERAS? sp.
Plate 94, figure 9

Cyrtoconic brevicones are rare in strata younger than the Devonian, and our collections contain only one of them. It is an internal mold of four camerae of a phragma-

---

EXPLANATION OF PLATE 95

All specimens, except those illustrated by figures *1–3* and *18–20*, are from upper part of the Barnett shale about 15 miles southeast of Llano, Texas. The specimen represented by figures *1–3* is from the Pitkin limestone near Saint Joe, Arkansas; and that represented by figures *18–20* is from the Bordley shale at the head of Moore Close Gill, Malham, northern England.

FIGS. *1–3*—*Cravenoceras* cf. *C. hesperium* Miller and Furnish, ×1½. (p. 669)
4–6—*Cravenoceras nevadense* Miller and Furnish. A small well preserved specimen, ×3. (p. 657)
7–9—*Cravenoceras hesperium* Miller and Furnish? An immature individual, ×3. (p. 656)
10–12—*Cravenoceras nevadense* Miller and Furnish. A small specimen, ×3. (p. 657)
13–15—*Cravenoceras hesperium* Miller and Furnish? A specimen that shows the juvenile portions of the conch, ×5. (p. 656)
16, 17—*Goniatites choctawensis* Girty. A small specimen, ×5. (p. 658)
18–20—*Cravenoceras malhamense* (Bisat). A topotype of the genotype, ×3. [This specimen was collected by E. W. J. Moore, and it is now at the State Univ. of Iowa, where its catalogue no. is 6979. (p. 656)

cone that is slightly but distinctly curved longitudinally, rapidly expanded orad, and subcircular in cross section. The maximum overall length of this specimen is about 19 mm. The cross section, which has been somewhat modified by distortion during preservation, increases in diameter from about 12 mm. near the adapical end of the specimen to about 19 mm. near its adoral end.

The septa are oblique to the long axis of the conch, and slope orad from the convex (ventral) to the concave (dorsal) side of the specimen. The septa are only moderately convex apicad. The siphuncle is small and subventral in position. At its passage through the septum that forms the adapical end of the specimen, the siphuncle is slightly less than 1 mm. in diameter and about 3 mm. from the venter.

Remarks.—This specimen represents such a small portion of the conch that it can not be compared satisfactorily with other forms. Superficially, at least, it seems to resemble the adapical portion of the specimen from the Caney shale of Oklahoma that Girty (1909, p. 49, pl. 10, figs. 1–1b) illustrated and described as *Cyrtorizoceras? hyattianum.*

Occurrence.—Upper part of Barnett formation about 5000 feet N. 54° W. from the point where the county road from Mason to White's Crossing crosses Honey Creek, which itself is about 8 miles by road southwest of Mason, Mason County, Texas.

Figured Specimen.—U. S. National Museum.

ENDOLOBUS sp.
Plate 94, figures 7, 8

One of the two coiled nautiloids that we have from the Barnett belongs in the genus *Endolobus.* It is fragmentary and only moderately well preserved. This specimen represents part of the adapical two volutions of the phragmacone. The figured portion of it has an overall length of about 51 mm., and near its adoral end the conch is about 40 mm. wide and 23 mm. high. The whorls are subrectangular in cross section as they are depressed dorsoventrally, somewhat flattened ventrally and laterally, and only slightly impressed dorsally.

The umbilicus is large and perforate. The perforation appears to be oval in shape, and its longer diameter is a little more than 4 mm. The umbilical shoulders are rounded and indefinite, and the umbilical walls only moderately steep.

The test of the extreme adapical portion of the conch bears reticulate ornamentation. At least the dorsolateral zones of the conch are prominently longitudinally lirate, and the lateral zones nodose. The nodes are low and rounded.

The camerae are rather short. The sutures form shallow, broadly rounded ventral, lateral, and dorsal lobes, and there is a small V-shaped annular lobe in the center of the dorsal lobe. The siphuncle is small and subcentral but distinctly closer to the venter than to the dorsum.

Remarks.—Inasmuch as this specimen represents only the inner volutions of the conch and is none too well preserved, detailed comparisons with similar forms are not possible.

Occurrence.—Upper part of Barnett formation about 5000 feet N. 54°W. from the point where the county road from Mason to White's Crossing crosses Honey Creek, which itself is about 8 miles by road southwest of Mason, Mason County, Texas.

Figured Specimen.—U. S. National Museum.

DISCITOCERAS TEXANUM Miller and Youngquist n. sp.
Plate 94, figure 6

This species is based on a single specimen which represents the adapical half of each of the first two volutions of a phragmacone. The portion of the inner volution that is preserved is largely testiferous, whereas that of the outer volution is mostly decorticated. The maximum diameter measured from the adoral end of the venter across the umbilicus to the opposite side of the specimen is almost 30 mm.

The umbilicus is large and open. Its diameter is equal to about two-fifths that of the conch. The umbilical perforation is oval in shape, and its two diameters are about 5 mm. and 6 mm.

The extreme adapical portion of the conch appears to be circular (or essentially so) in cross section. However, at the adoral end of the first half-volution, the cross section is more or less octagonal and higher than

wide—the ventral zone is slightly convex on the internal mold but is distinctly concave on the test due to the development of sharp ventrolateral ridges. As shown by text figure 1, during later ontogenetic development the conch became progressively higher and more compressed, and it developed broad lateral zones that converge ventrally.

The test of at least the first half-volution of the conch bears a sharp longitudinal ridge on the umbilical shoulder, a second one on the median lateral zone, and a third on the ventrolateral zone—the last is the most prominent. Also, there are numerous fine transverse lines on at least the umbilical wall—some of them appear to slope slightly apicad toward the dorsum.

The camerae are short, and in the adoral half-volution of the holotype there are about 23 of them. On the extreme adapical portion of the conch, the sutures appear to form simple circles. On the adoral portion, each forms a rather high flattened ventral saddle with a broadly rounded asymmetrical lateral lobe on either side of it, a slight umbilical saddle, and almost certainly a dorsal lobe (due to the impressed zone).

The siphuncle is small, at least at its passage through the septa. Except possibly in the extreme adapical portion of the phragmacone, it is located fairly close to the venter.

Remarks.—This form is not very similar to any genotype with which we are familiar, but it is perhaps closest to the type species of *Discitoceras*, *D. costellatum* (M'Coy) of the Lower Carboniferous of Ireland. Furthermore, it does not resemble the only congeneric form known from North America, *D. sulcatum* (Sowerby) of the Meramec of Kentucky. It is superficially similar to *D. discum* (Sowerby) of the Viséan of England and possibly Belgium, and is very much like some undescribed specimens in the collections of the State University of Iowa from Bisat's P_1 zone in the Viséan of the Isle of Man.

Occurrence.—Upper part of Barnett formation about 5000 feet N. 54°W. from the point where the county road from Mason to White's Crossing crosses Honey Creek, which itself is about 8 miles by road southwest of Mason, Mason County, Texas.

Holotype.—U. S. National Museum.

Genus CRAVENOCERAS Bisat, 1928
Genotype: *Homoceras malhamense* Bisat

The Barnett shale and related formations in North America have yielded abundant ammonoids of a rather generalized nature that seem to resemble the genotypes of *Anthracoceras* Frech, *Cravenoceras* Bisat, *Cravenoceratoides* Hudson, *Homoceras* Hyatt, *Homoceratoides* Bisat, and *Nuculoceras* Bisat, Of these several genera, *Homoceras* has priority, but unfortunately it was based on

FIG. *1*—Diagrammatic cross section of the internal mold of the holotype of *Discitoceras texanum*, n. sp., ×2.

a small immature specimen whose precise zone and locality are not known—it came from one of three localities in Yorkshire. Bisat (1924, pp. 102–103) has emphasized that the mature characters of this form can not be determined with certainty, and therefore we are reluctant to refer to the genus any specimens other than the one on which it was based. Furthermore, none of our numerous specimens seem to have nodose umbilical margins during early ontogenetic development, as does the genoholotype, and also the sutures of our specimens form a relatively narrow ventral lobe the flanks of which are not strongly divergent orad.

The genotype of *Anthracoceras*, *Dimorphoceras* (*Anthracoceras*) *discus* Frech, and that of *Nuculoceras*, *N. nuculum* Bisat (as illustrated by Hind, 1918, pl. 16, figs. 8, 8a, 9, 9a, 12–12b), also have sutures in which the flanks of the ventral lobe are rather strongly

divergent. Furthermore, the transverse lirae on the test of *N. nuculum* and those on the type species of *Homoceratoides, H. prereticulatum* Bisat, are strongly sinuous—the sutures of *H. prereticulatum* are not known. The genotype of *Cravenoceratoides, Goniatites nitidus* Phillips, bears fairly prominent transverse ribs.

The type species of *Cravenoceras, Homoceras malhamense* Bisat (pl. 95, figs. 18–20, of the present publication), has sutures and test ornamentation that are very much like those of the American specimens under consideration. That is, the ventral lobe of the sutures is relatively narrow and its flanks are almost parallel; and the surface markings of the test consist of lirae that are essentially straight and directly transverse. However, the umbilicus of that form is considerably larger and the conch somewhat more depressed than in most of our specimens.

In summary, it seems to us that all of these genera are very closely similar. Our specimens resemble the genotype of *Cravenoceras* insofar as sutures and test ornamentation are concerned, but most of them differ in the shape of the whorls and the size of the umbilicus. It is generally believed that the nature of the sutures and the surface markings of the test are of relatively great taxonomic value in comparison to other features. Therefore, we are referring the American specimens under consideration to *Cravenoceras* rather than to any of the other closely related genera.

Cravenoceras differs from *Goniatites*, with which it occurs in direct association, in America, at least, particularly in the shape of the first lateral saddles of the sutures. In *Cravenoceras* those saddles are broadly rounded throughout ontogenetic development, whereas in *Goniatites* at maturity they are very narrowly rounded, subangular, or even angular. *Gastrioceras*, of which the genotype is *Goniatites listeri* (Martin) [as illustrated by Phillips, 1836, pl. 20, figs. 1, 1a] differs particularly in that its umbilical shoulders are nodose at maturity.

Bisat (1928, p. 132) indicated that *Cravenoceras* is limited to the zone of *Eumorphoceras*, which in the eastern hemisphere is stated to occur above the beds that contain *Goniatites*. However, it is now clear that *Eumorphoceras, Goniatites*, and *Cravenoceras* (as interpreted by us) all occur together in the Barnett shale of north-central Texas, the Caney shale of Oklahoma, and probably the White Pine shale of southeastern California. *Cravenoceras* is both widespread and abundant in the Middle and/or Upper Mississippian (and equivalent strata) of both North America and Eurasia, and forms that seem to belong in it occur also in American Lower Pennsylvanian beds.

CRAVENOCERAS HESPERIUM Miller and Furnish?

Plate 95, figures 7–9, 13–15

?Nuculoceras incisum [part] PLUMMER and SCOTT, 1937, Texas Univ. Bull. 3701, pp. 15, 29, 30, 33, 106–108, 109, 113, 383, 384, 399, pl. 7, figs. 7–9, 11–14 [not 10].

?Nuculoceras barnettense [part?] PLUMMER and SCOTT, 1937, Texas Univ. Bull. 3701, pp. 15, 33, 106, 108–109, 110, pl. 7, figs. 15–18.

?Cravenoceras hesperium MILLER and FURNISH, 1940, Jour. Paleontology, vol. 14, pp. 356, 373, 374–375, pl. 49, figs. 1–8.

The collections contain three small specimens that have subglobular conchs, small umbilici, transverse lirae, and sutures that are typical of *Cravenoceras*. At least the two that are figured are completely septate, and presumably they represent immature portions of the conch. One of them (fig. 14) is broken in such a way as to show the shape of four or five volutions. The wide conch and small umbilicus of these forms suggest a relationship to *C. hesperium*, but inasmuch as all three specimens are believed to be immature, we are uncertain in regard to their precise affinities.

Occurrence.—Barnett formation at two localities in central Texas. Both of the figured specimens are from about 1900 feet due west from a point 1.93 miles south of the Honey Creek crossing of the Llano-Click road, which is about 15 miles by road southeast of Llano, Llano County. Our third Barnett specimen was found about 5000 feet N. 54°W. from the point where the county road from Mason to White's Crossing crosses Honey Creek which itself is about 8 miles by road southwest of Mason, Mason County. Plummer and Scott (1937, pp. 107, 108) indicate that forms which may be conspecific occur also in the same formation about 5 miles west of Lampasas, Lampasas County; and 1 mile south of Richland Springs, San Saba County, Texas.

CRAVENOCERAS NEVADENSE Miller and Furnish

Plate 95, figures 4–6, 10–12; plate 96, figures 4–6, 13–15; plate 100, figures 18, 19

Nuculoceras incisum [part ?] PLUMMER and SCOTT, 1937, Texas Univ. Bull. 3701, pp. 15, 29, 30, 33, 106–108, 109, 113, 383, 384, 399 [not pl. 7, figs. 7–14].

Nuculoceras barnettense [part ?] PLUMMER and SCOTT, 1937, Texas Univ. Bull. 3701, pp. 15, 33, 106, 108–109, 110 [not pl. 7, figs. 15–18.

Cravenoceras richardsonianum [part] PLUMMER and SCOTT, 1937, Texas Univ. Bull. 3701, pp. 15, 116, 261–262, 265, 379, 380, 383, 384, 399, pl. 8, figs. 12–16.

Cravenoceras? nevadense MILLER and FURNISH, 1940, Jour. Paleontology, vol. 14, pp. 356, 373, 374, 375–376, pl. 49, figs. 9–13.

We refer to this species specimens that have subglobular conchs, open umbilici, growth lines and constrictions that are directly transverse and almost straight, and sutures that are typical of what we regard as *Cravenoceras*. In these specimens the whorls tend to become relatively higher and narrower during ontogenetic development, and at full maturity there is a certain amount of variation insofar as the width of conch is concerned. The diameter of the umbilicus also varies, and in some cases (for example, pl. 96, fig. 15) it begins to approach that of *C. kingii* (Hall and Whitfield). There seems to be gradation between *C. nevadense* and *C. kingii* and between the former and *C. hesperium* Miller and Furnish, and it may well be that all three should be regarded as conspecific, in which case Hall and Whitfield's name would have priority. In *C. richardsonianum* (Girty) of the Caney shale of Oklahoma, the conch is more narrowly rounded ventrally than in any of the numerous Barnett specimens available for study. Some of these are similar to the genotype, *C. malhamense* (Bisat) of northern England (cf. pl. 95, figs. 10–12 and 18–20).

Occurrence.—Abundant in Barnett formation at three localities in central Texas: (1) about 1900 feet due west from a point 1.93 miles south of the Honey Creek crossing of the Llano-Click road, which is about 15 miles by road southeast of Llano, Llano County (pl. 95, figs 4–6, 10–12); (2) about 5000 feet N. 54°W. from the point where the county road from Mason to White's Crossing crosses Honey Creek, which itself is about 8 miles by road southwest of Mason Mason County (pl. 96, figs. 4–6, 13–15); and (3) about 14 feet below the Barnett-Marble Falls contact some 2½ miles south-southeast of San Saba along San Saba-Chappel road, San Saba County (pl. 100, figs. 18, 19). Also, we refer with question to this species a small specimen from the Barnett shale along the Bend-San Saba road some 7 miles east of San Saba, Texas. Plummer and Scott (1937, pp. 107, 108) indicate that forms which are probably conspecific occur also in the same formation about 5 miles west of Lampasas, Lampasas County; and 1 mile south of Richland Springs, San Saba County, Texas. The original type specimens of this species came from the White Pine shale of east-central Nevada.

Repository.—U. S. National Museum.

CRAVENOCERAS SCOTTI Miller and Youngquist, n. sp.

Plate 96, figures 7, 8; plate 97, figures 22–24

The Barnett shale has yielded three specimens that are referable to *Cravenoceras* but do not seem to belong in any of the established species of that genus. The best individual (pl. 96, figs. 7, 8) is chosen as the holotype. All three are rather well preserved internal molds that are septate throughout.

The conch is subglobular, and the whorls low and broad. The maximum diameter of the holotype measures about 18 mm., and near its adoral end the conch is about 15 mm. wide and 5 mm. high. The whorls are broadly rounded ventrally and ventrolaterally and impressed dorsally, the umbilical shoulders are abrupt, and the umbilical walls are steep. The umbilicus is moderately large, and its diameter is equal to about a third that of the conch—the umbilicus of the holotype attains a maximum diameter of a little more than 6 mm.

The surface of the internal mold bears low rounded ribs that are directly transverse to the long axis of the conch and are almost straight, though they curve slightly orad as they cross the broad ventral zone. Also, in at least the internal mold, there are prominent sinuous transverse constrictions parallel to the ribs. In all three specimens, there are three of these constrictions in the outer volution.

At maturity each external suture forms a

rather narrow almost straight-sided rather prominently divided ventral lobe, and on either side of it a rounded U-shaped first lateral saddle (which is slightly contracted near mid-height), a more or less V-shaped acuminate first lateral lobe, a broad rounded second lateral saddle, and a small acuminate lobe on the umbilical wall.

Remarks.—The most distinctive characteristics of this species are its wide conch, rather large umbilicus, and transverse ribs. The general characters of the conch serve to distinguish it from the other congeneric forms known from America, at least. The unfigured paratype is of about the same size as the holotype, which it resembles very closely.

The specific name is given for the late Professor Gayle Scott of Texas Christian University whose work on the ammonoids is well known.

Occurrence.—All three specimens came from the upper part of Barnett formation about 5000 feet N. 54°W. from the point where the county road from Mason to White's Crossing crosses Honey Creek, which itself is about 8 miles by road southwest of Mason, Mason County, Texas.

Types.—U. S. National Museum.

GONIATITES CHOCTAWENSIS Shumard

Plate 95, figures 16, 17; plate 96, figures 1–3, 9–12; plate 97, figures 1–21; plate 98, figures 1–13; plate 99, figures 1–19

Goniatites choctawensis SHUMARD, 1863, St. Louis Acad. Science, Tr., vol. 2, pp. 109–110; SMITH, 1903, U. S. Geol. Survey Mon. 42, pp. 67–68, 144; GIRTY, 1909, U. S. Geol. Survey Bull. 377, pp. 9, 10, 54, 56, 58, 59–62, 63, 64, 102, pl. 13, figs. 1–11b; GIRTY, 1911, U. S. Geol. Survey Bull. 439, pp. 12, 13, 18, 19, 20, 22, 25, 97–99, 100, pl. 15, figs. 1–7; GIRTY, 1915, U. S. Geol. Survey Bull. 593, pp. 14, 129–130, pl. 5, figs. 4, 5; CRONEIS, 1930, Arkansas Geol. Survey Bull. 3, pp. 55, 64, 71; GIRTY, 1934, Am. Assoc. Petroleum Geologists, Bull., vol. 18, p. 1543; PLUMMER and SCOTT, 1937, Texas Univ. Bull. 3701, pp. 15, 29, 30, 106, 107, 113–114, 381, 383, 384, 399, pl. 7, figs. 3–6; SCHUCHERT, 1943, Stratigraphy of the eastern and central United States, pp. 852, 912.

Glyphioceras incisum [part?] HYATT, 1893, Texas Geol. Survey, Ann. Rept. 4, pp. 471–472, pl. 47, figs. 44–48; [part?] SMITH, 1897, California Acad. Science, Proc., 3d. ser., Geol., vol. 1, pp. 111–122, pls. 13–15; [part?] PLUMMER and MOORE, 1922, Texas Univ. Bull. 2132, pp. 29, 30.

Glyphioceras cumminsi HYATT, 1893, Texas Geol. Survey, Ann. Rept. 4, pp. 467–471, pl. 47, figs. 33–43; [part?] PLUMMER and MOORE, 1922, Texas Univ. Bull. 2132, pp. 29, 30.

Goniatites kentuckiensis MILLER, 1899, North American geology and palaeontology for the use of amateurs, students, and scientists, pp. 439–440, text fig. 740; MILLER and GURLEY, 1896, Illinois State Mus. Nat. Hist. Bull. 11, pp. 40–41, pl. 5, fig. 1; SMITH, 1903, U. S. Geol. Survey Mon. 42, pp. 14, 77, 81, 144, pl. 17, fig. 1; PLUMMER and SCOTT, 1937, Texas Univ. Bull. 3701, p. 114; MILLER and FURNISH, 1940, Jour. Paleontology, vol. 14, pp. 356, 357, 361–363, pl. 46, figs. 1–13; GORDON, 1944, Am. Assoc. Petroleum Geologists, Bull., vol. 28, p. 1633; SHIMER and SHROCK, 1944, Index fossils of North America, p. 571, pl. 234, figs. 9, 10.

Goniatites striatus [part] SMITH, 1903, U. S. Geol. Survey Mon. 42, pp. 14, 15, 62, 63, 66, 67, 68, 69, 70, 77, 79, 80–81, 87, 144, pl. 10, figs. 1–11; pl. 26, figs. 6–13.

Goniatites crenistria [part] SMITH, 1903, U. S. Geol. Survey Mon. 42, pp. 14, 15, 63, 66, 67, 68–76, 79, 80, 81, 144, pl. 10, figs. 12–16; pl. 14, figs. 1–12; pl. 15, figs. 1–9; pl. 16, figs. 1a–1j; pl. 26, figs. 1–5; CRONEIS, 1930, Arkansas Geol. Survey, Bull. 3, pp. 55, 71; SHIMER and SHROCK, 1944, Index fossils of North America, p. 571, pl. 234, figs. 4, 5.

Goniatites sp. GIRTY, 1918, U. S. Geol. Survey Prof. Paper 110, p. 39.

?Glyphioceras n. sp., PLUMMER and MOORE, 1922, Texas Univ. Bull. 2132, pp. 29, 44, pl. 7, fig. 12.

Glyphioceras (*Goniatites*) *choctawensis* PLUMMER and MOORE, 1922, Texas Univ. Bull. 2132, pp. 29, 30.

Goniatites subcircularis CRONEIS, 1930, Arkansas Geol. Survey Bull. 3, pp. 56, 71.

Goniatites newsomi CRONEIS, 1930, Arkansas Geol. Survey Bull. 3, pp. 56, 71.

Nuculoceras incisum [part] PLUMMER and SCOTT, 1937, Texas Univ. Bull. 3701, pp. 15, 29, 30, 33, 106–108, 109, 113, 383, 384, 399, pl. 7, fig. 10 [not 7–9, 11–14].

The type species of the genus *Goniatites* is *Conchyliolithus Nautilites sphaericus* Martin of the Lower Carboniferous of England and possibly Ireland, Belgium, and Germany. Specimens that are sufficiently similar to this genotype to be regarded as congeneric with it occur in some abundance in the Barnett shale of central Texas as well as in the Helms formation of west Texas, the Caney shale of Oklahoma, the "Meramec" of Kentucky, and the Moorefield, Ruddell, Batesville, and Fayetteville formations of Arkansas (and possibly the White Pine shale of southeastern California). Specimens from these American localities show a great deal of variation. Some have broader conchs than others, some are almost evenly rounded ventrally and ventrolaterally,

whereas others are flattened ventrally and laterally and relatively narrowly rounded ventrolaterally. In all the umbilicus is closed during rather early ontogenetic development, but in the adoral portions of large individuals it is open. The sutures also reveal gradational differences in addition to those due to ontogenetic development. A difference is particularly noticeable in the shape of the first lateral saddle which in some specimens is much more narrowly rounded than in others at the same diameter.

Fortunately we now have available for direct comparisons a considerable number of specimens from the five American localities under consideration. In almost all of the numerous mature specimens from the Caney of Oklahoma, the first lateral saddles of the sutures are subangular and the first lateral lobes are acuminate. Also, the surface of the test is crenulate as it bears numerous small longitudinal lirae and very fine sinuous transverse growth lines.

The majority of the Kentucky specimens have broader conchs than do those from Oklahoma. Also, the surficial ornamentation of these forms appears to consist of relatively large longitudinal lirae, and the first lateral saddles of the sutures are narrowly rounded (rather than subangular) until a very late stage of ontogenetic development.

Most of the numerous specimens from the Barnett of central Texas have sutures like those of the Kentucky forms. However, their conchs are relatively narrow (though there are exceptions, for example, pl. 99, figs. 1, 2). The ornamentation of some of them (pl. 99, fig. 17) consists primarily of almost straight transverse lirae, whereas that of others (pl. 95, fig. 17; pl. 98, fig. 7) is predominantly of longitudinal lirae. Essentially all of the Arkansas and west Texas specimens available to us are small, and therefore we are not able to determine the nature of their mature surface ornamentation.

Most of our specimens do not retain the surface markings of the test, and therefore it is not practicable to divide them on that basis (as is commonly done by European paleontologists). Furthermore, the differences in the form of the conch and the shape of the sutures, like the differences in the constrictions, appear to be completely gradational. Accordingly, it seems to us that with the present data it is difficult if not impossible to delimit effectively more than one species among all these specimens. Therefore, we are using Shumard's name, *Goniatites choctawensis*, for the entire group, because it has priority. However, we recognize that the extreme variants in the collections under consideration may well be worthy of varietal differentiation. Although Shumard's types have been lost, presumably they possessed the relatively narrow conch, crenulate ornamentation, and subangular first lateral saddles characteristic of the great majority of Caney specimens, which can therefore be termed *G. choctawensis choctawensis* (pl. 98, figs. 4, 5).

The obese forms with coarse longitudinal lirae, which predominate in the "Meramec" of Kentucky can be designated *G. choctawensis kentuckiensis* Miller. Cloud and Barnes (manuscript in press) designated as the holotype of Hyatt's "*Glyphioceras cumminsi*" a specimen with a relatively narrow conch and fine but prominent longitudinal lirae, and the name *G. choctawensis cumminsi* should therefore be used for specimens like that shown by figures 6–8 on our plate 98. No name seems to be available for the variety typified by figures 16–19 on plate 99 and characterized by a relatively narrow conch, a transversely (but not longitudinally) lirate test, and sutures with narrowly rounded first lateral saddles at maturity, and therefore we here propose to call it *G. choctawensis barnettensis*.

The usual difficulties of intermediate forms and the cumbersomeness of trinomials will of course be encountered in connection with these four varieties. For these reasons and because most of the specimens do not retain the test and the varieties apparently have no stratigraphic value more precise than that of the species, most geologists will probably not find subdivisions of the species particularly useful.

Goniatites s. s. is both widespread and abundant in the eastern hemisphere as well as in this country. In Europe, where Lower Carboniferous ammonoids have been given a great deal of consideration, the genus is said to be limited to the upper Viséan. Presumably the beds in which it occurs here are essentially contemporaneous.

Occurrence.—Barnett formation at four localities in central Texas: (1) about 1900 feet due west from a point 1.93 miles south of the Honey Creek crossing of the Llano-Click road, which is about 15 miles by road southwest of Llano, Llano County (pl. 95, figs. 16, 17); (2) about 5000 feet N. 54°W. from the point where the county road from Mason to White's Crossing crosses Honey Creek, which itself is about 8 miles by road southwest of Mason, Mason County (pl. 96, figs. 1–3, 9–12; pl. 97, figs. 8–10, 14–21; pl. 98, figs. 10, 11); (3) about 2½ miles south-southeast of San Saba along the San Saba-Chappel road, San Saba County (pl. 97, figs. 1–7, 11–13; pl. 99, figs. 1–19; and (4) about 3100 to 3200 feet S. 14°W. from the southwest end of the slab at White's Crossing of the Llano River, which is about 10 miles by road southwest of Mason, Mason County (pl. 98, figs. 1–3, 6–9, 12, 13). Also Plummer and Scott have recorded the occurrence of specimens some of which are probably conspecific at the following additional localities in the Barnett formation of Texas: (1) along Espey Creek, 4 miles southwest of Lampasas, Lampasas County; (2) 5 miles west of Lampasas, Lampasas County; and (3) 1 mile south of Richland Springs, San Saba County.

Specimens that belong in this species (as we are interpreting it) also occur in the Helms formation of west Texas; the Caney shale of Oklahoma (pl. 98, figs. 4, 5); the Moorefield, Ruddell, Batesville, and Fayetteville formations of Arkansas; the "Meramec" of Kentucky; and probably the White Pine shale in southeastern California.

Figured Specimens.—U.S. National Museum (except figs. 4, 5 on pl. 98, which is in the John Britts Owen Collection at The State University of Iowa, catalogue number 6980).

LYROGONIATITES CLOUDI Miller and Youngquist, n. sp.
Plate 94, figures 1–3

At one locality the Barnett yielded about a dozen conspecific specimens that belong in *Lyrogoniatites* but seem not to be referable to any previously known species of that genus. The conch of this form is moderately large, and it attains a diameter of at least 35 mm. It is subglobular in shape as its whorls are depressed dorsoventrally, broadly rounded ventrally, ventrolaterally, and laterally, abruptly rounded dorsolaterally, impressed dorsally, and low helmet-shaped in cross section. The figured specimen is about 30 mm. in diameter, and near its adoral end its conch is about 16 mm. wide and 9 mm. high. The living chamber is more than a volution in length. The largest of the specimens attains a maximum diameter of about 34 mm.

The umbilicus is large and its diameter is equal to about one-half that of the specimen. The maximum diameter attained in the figured specimen is about 15 mm. The umbilical shoulders are abruptly rounded and the umbilical walls are steep.

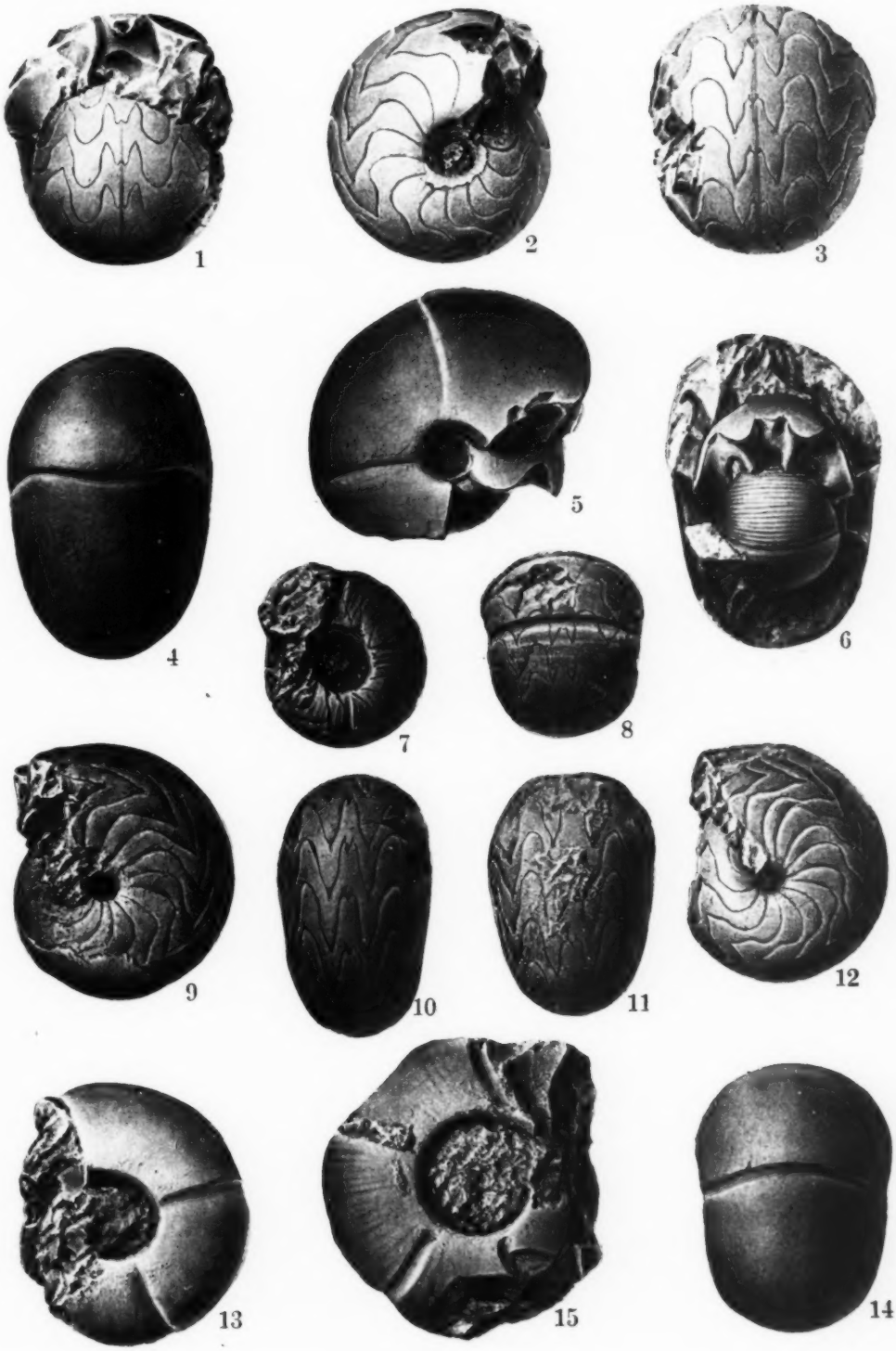
The surface of the test bears rather prominent longitudinal lirae which do not seem to be present on the umbilical walls. On the outer surface (from umbilical shoulder to umbilical shoulder) of the adoral portion of the figured specimen, there are about 23 lirae. The specimens also bear traces of transverse increments of growth. These form broad shallow rounded ventral and lateral sinuses and narrower ventrolateral salients. They are essentially parallel to the prominent constrictions, of which there are about three to a volution.

Only one of the type specimens reveals sutures, and they are not well preserved.

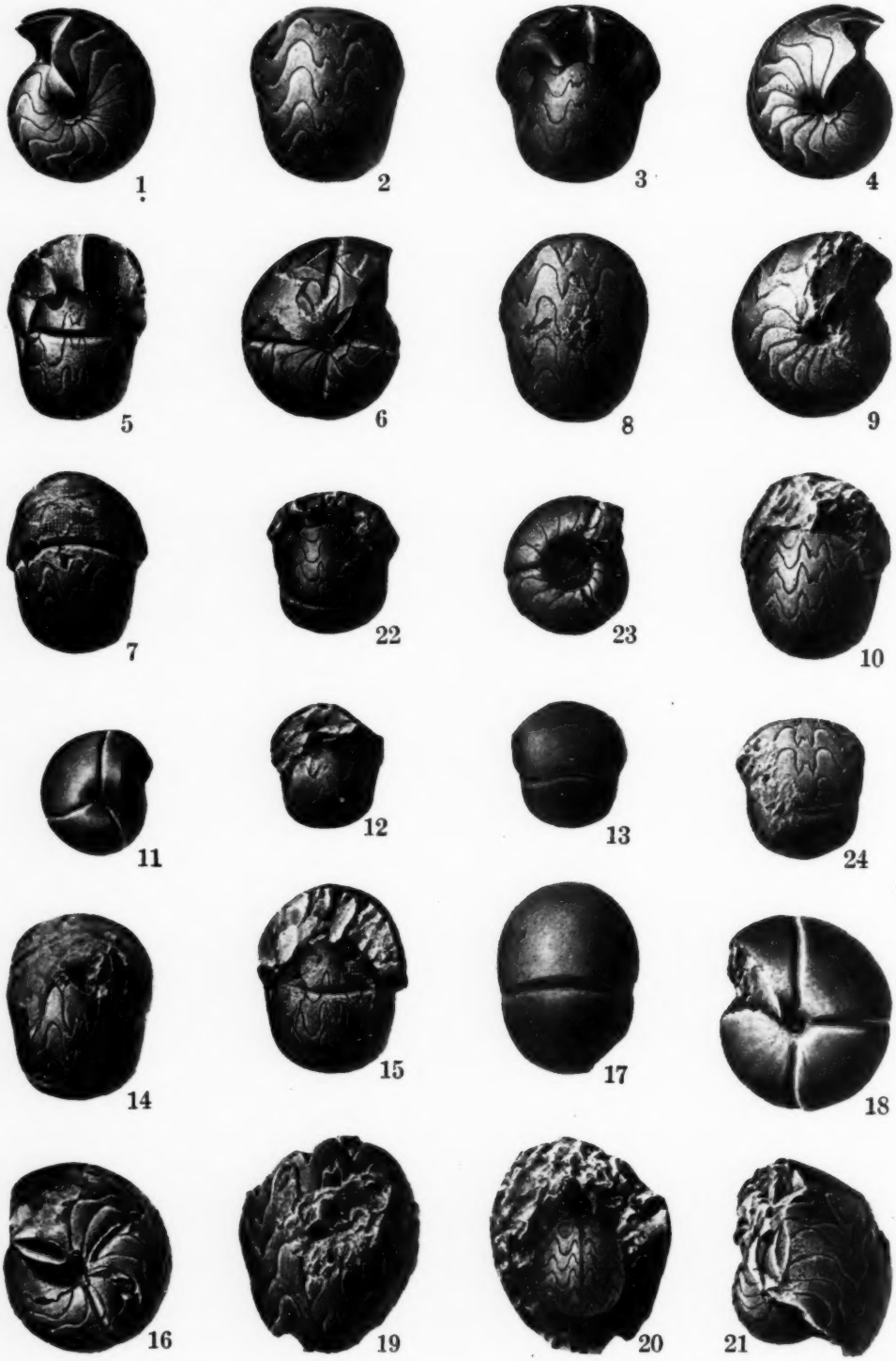
EXPLANATION OF PLATE 96

All specimens are from the upper part of the Barnett shale about 8 miles southwest of Mason, Texas.

FIGS. *1–3—Goniatites choctawensis* Shumard. A small specimen, ×5. (p. 658)
4–6—Cravenoceras nevadense Miller and Furnish, ×1½. (p. 657)
7, 8—Cravenoceras scotti, n. sp. The holotype, ×1½. (p. 657)
9–12—Goniatites choctawensis Shumard. Two specimens, ×1 (figs. *9*, *10*) and ×1½ (figs. *11*, *12*). (p. 658)
13–15—Cravenoceras nevadense Miller and Furnish. Two specimens, both ×1½. (p. 657)



Miller and Youngquist, Mississippian Cephalopoda



Miller and Youngquist, Mississippian Cephalopoda

However, each forms a narrow ventral lobe with almost parallel sides and on either side of it a rounded asymmetrically U-shaped first lateral saddle, a V-shaped first lateral lobe, a shallow broadly rounded second lateral saddle, and a small lobe on the umbilical wall.

Remarks.—This species resembles the genotype of *Lyrogoniatites*, *L. newsomi georgiensis* Miller and Furnish of the Floyd shale of Georgia, but it has a narrower conch and larger umbilicus. *L. entogonus* (Gabb) of the Barnett shale of Texas is also similar but it has broader whorls and a larger umbilicus. A closely similar, if not identical, form occurs in the Helms formation of west Texas.

We designate the figured specimen as the holotype. No trace of the sutures is visible on it. However, they can be seen on one of the paratypes at a diameter of about 17 mm.

Occurrence.—All of the type specimens of this species were collected by G. A. Cooper from blocks of limestone on the south side of a shallow borrow pit along the San Saba-Chappel road about 2½ miles south-southeast of San Saba, Texas. Cloud has informed us that these blocks are most probably from the lower third of the Barnett shale, as they were almost certainly taken from the pit. They also yielded a few moderately small specimens of *Gonitatites choctawensis* Shumard.

Types.—U. S. National Museum.

Genus EUMORPHOCERAS Girty, 1909
Genotype: *Eumorphoceras bisulcatum* Girty

When Girty (1909, pp. 67–68) established this genus, he noted that it is related to *Girtyoceras* (his "*Adelphoceras*"), and listed the criteria which in his opinion could be used to differentiate them. Since that time, the relationship between these genera has been questioned. It has been discussed by many paleontologists, for example, Bisat and Moore in England, Wedekind and Schmidt in Germany, Librovitch in Soviet Russia, and Plummer and Scott in this country. These authors have reached diverse conclusions.

The most recent discussion of the problem is by Moore (1946, pp. 393–395). He states that Girty's types

> are now known to be immature specimens and the differences between these genera, as stated by him, break down now that larger specimens are known.

In a consideration of the various criteria that might be used to differentiate the two, Moore indicates that the

> development of strong ribs as early as the second whorl is characteristic of *Eumorphoceras* and I [Moore] regard this as the essential difference between the two genera. In some forms of *Girtyoceras* there is ribbing but it is feeble and soon dies out. . . . As a rule the ribbing persists longer in *Eumorphoceras*.

After studying representatives of this genus, and of *Girtyoceras*, from several American and British localities, we have concluded that in small specimens there is more or less gradation between the two, and no single criterion can be used to differentiate them satisfactorily. Nevertheless, as noted by Moore, during rather early ontogenetic development there is a tendency for representatives of *Eumorphoceras* to develop relatively prominent lateral ribs; and as pointed out by Girty, small specimens of typical *Girtyoceras* have prominent sinuous transverse constrictions, and sutures in which the lobes are relatively acuminate.

European authors indicate that *Eumorphoceras* occurs in younger strata than does

---

EXPLANATION OF PLATE 97

All specimens are from the Barnett shale at two localities in central Texas. Those illustrated by figures *1–7* and *11–13* are from 2½ miles south-southeast of San Saba; those by figures *8–10* and *14–24* are from 8 miles southwest of Mason.

FIGS. *1–21*—*Goniatites choctawensis* Shumard. Figures *1–4*, a small specimen, ×4. Figures *5–7*, a septate individual, ×1½. Figures *8–10*, a subglobular specimen, ×1½. Figures *11–13*, a small individual, ×2. Figures *14–16*, a well preserved internal mold, ×1½. Figures *17*, *18*, a specimen retaining the living chamber, ×1½. Figures *19–21*, a fragmentary specimen showing the internal whorls, ×3. (p. 658)

22–24—*Cravenoceras scotti*, n. sp. The better paratype, ×1½. (p. 657)

Girtyoceras. However, in both of its known occurrences[4] in this country, the Caney shale of Oklahoma and the Barnett shale of Texas, *Eumorphoceras* is found in direct association with *Girtyoceras*, and insofar as we have been able to ascertain there is no known difference in their stratigraphic range here. *Girtyoceras* is the more abundant of the two genera in this country, and it is known from several localities that have so far not yielded *Eumorphoceras*, but in every case there seems to be no good reason to believe that the beds from which *Girtyoceras* but not *Eumorphoceras* has been collected differ in age from those that are known to carry both genera. Although we can now suggest rather definite correlations of the strata which contain *Eumorphoceras* in this country with other American goniatite-bearing beds, it is not possible for us to be certain as to their position with reference to the classical upper Mississippi Valley sections. The difficulty stems from the fact that no goniatite faunas are known from the type areas of either the Meramec or the Chester, and very few specimens have been collected from the Osage. Tentatively, we regard the zone of *Eumorphoceras* in America as Meramec in age.

The collections that are available to us for study contain many representatives of *Eumorphoceras* from both this country and abroad. Those from the Barnett shale of Texas seem to be divisible into two species, one of which is characterized by a relatively globular conch and a rounded ventral zone, whereas the other has a subdiscoidal conch that is flattened ventrally. The first of these forms is referable to *E. bisulcatum* Girty, and for the second we propose to establish a new species, *E. plummeri*.

EUMORPHOCERAS BISULCATUM Girty
Plate 100, figures 9–17

Eumorphoceras bisulcatum GIRTY, 1909, U. S. Geol. Survey Bull. 377, pp. 10, 67–70, pl. 11, figs. 15–19a; [part] WEDEKIND, 1918, Palaeontographica, Bd. 62, p. 139; ?GIRTY, U. S. Geol. Survey Prof. Paper 110, p. 39; MORGAN, 1924, [Oklahoma] Bureau Geol. Bull. 2, p. 54; BISAT, 1924, The Naturalist, p. 87; [part?] ——, 1924, Yorkshire Geol. Soc., Pr., n. ser., vol. 20, pp. 72, 96–98, 99, 100, 117, pl. 6, figs. 1–5; pl. 10, fig. 12; [part?] SCHMIDT, 1925, Preuss. Geol. Landesanstalt, Jahrb., Bd. 45, pp. 497, 500, 501, 507, 511, 512, 530, 575, 577, 578, 579, 582, 583, 584–585, pl. 22, fig. 5; pl. 25, figs. 2, 3; [part?] JACKSON, 1927, Manchester Geol. Assoc., Jour., vol. 1, pp. 17, 23, 24, 26, 27, 28, 29, 30, 31, 32; ?WADDINGTON, 1927, Manchester Geol. Assoc., Jour., vol. 1, pt. 1, p. 42; [part?] BRAY, 1927, Manchester Geol. Assoc., Jour., vol. 1, pp. 52, 53, 54–55; [part?] BISAT, 1928, C. R. Cong. l'avanc. études Stratigr. Carbon. Heerlen, 1927, pp. 127, 132, pl. 6; MAILLIEUX and DEMANET, 1929, Soc. Belge Géol., Bull., t. 38, p. 129, tab. 1; [part?] SCHMIDT, 1929, Tierische Leitfossilien des Karbon, Gürich's Leitfossilien, Lief, 6, pp. 70–71, pl. 19, figs. 5, 6; [part?] BISAT, 1930, Leeds Geol. Assoc., Trans., pt. 20, p. 31; DELÉPINE, 1930, Soc. géol. France, Livre Jubilaire (1830–1930), t. 1, p. 228; [part?] DORLODOT, 1930, Inst. géol. Univ. Louvain, Mém., t. 6, fasc. 1, pp. 7, 22, 48, 49, tab. B; [part?] DELÉPINE, 1930, Inst. géol. Univ. Louvain, Mém., t. 6, fasc. 1, pp. 57–58, 62, 63, pl. 1, figs. 1–5; [part?] JACKSON, 1930, Manchester Geol. Assoc., Jour., vol. 1, pt. 2, pp. 73, 75; ?MOORE, 1930, Manchester Geol. Assoc., Jour., vol. 1, pp. 106, 107, 108; ?CRONEIS, 1930, Arkansas Geol. Survey, Bull. 3, p. 56; ?BISAT, 1931, Leeds Geol. Assoc., Trans., vol. 5, pp. 27, 30; [part?] DELÉPINE, 1931, C. R. Cong. Soc. Savantes, 1928, Lille, p. 135; [part] MAILLIEUX, 1933, Mus. royal Hist. nat. Belg., Patrimoine, pp. 100, 102, pl. 10, fig. 139; [part?] BISAT, 1933, Geol. Assoc., Proc., vol. 44, pt. 3, p. 256, pl. 30; ?VERHOOGEN, 1934, Soc. Géol Belg., Ann., t. 58, Bull. 2, pp. B98, B99; [part?] SCHMIDT, 1934, Preuss. Geol. Landesanstalt, Jahrb., Bd. 54, pp. 442–451, 454, 455, 459–461; ?BISAT, 1934, Leeds Geol. Assoc., Trans., vol. 5, pt. 2, p. 115; ?HUDSON, 1934, Leeds Geol. Assoc., Trans., vol. 5, pt. 2, pp. 119, 120, 121, 122, 123; ?DELÉPINE, 1935, Soc. géol. France, Bull., 5e sér., t. 5, pp. 172, 184–185, pl. 8, figs. 5, 6; ?WOOD, 1936, Liverpool Geol. Soc., Pr., vol. 17, pt. 1, pp. 16, 17, 23; ?DEMANET, 1936, Mus. royal Hist. nat. Belg., Bull., t. 12, no. 44, pp. 1, 2, 4, 5, 6, pl. 2, fig. 5; [part?] BISAT, 1936, Internat. Geol. Cong., Rept. 16th sess., vol. 1, pp. 531, 534, table 1; ?DELÉPINE, 1937, C. R. deuxième Cong. l'études Stratig. Carbon—Heerlen, 1935, pp. 145, 152, 153; [part] PLUMMER and SCOTT, 1937, Texas Univ. Bull. 3701, pp. 15, 16, 175–176, 378, 382–384, 399, 401, pl. 38, fig. 7 [not 4–6]; [part?] HUDSON and MITCHELL, 1937, Geol. Surv., Summ. Prog. for 1935, pt. 2, p. 5; [part?] HUDSON, 1938, Geol. Assoc., Proc., vol. 49, pt. 3, pp. 316, 321–322; [part?] HUDSON, 1938, Geol. Assoc., Proc., vol. 49, pt. 4, p. 357; [part?] HUDSON and EDWARDS, 1938, Geol. Assoc., Proc., vol. 49, pt. 4, pp. 358, 362, 363, 371; [part?] SCHMIDT, 1938, Geol. niederrheinisch-westfälischen Steinkohlengebietes im auftrage westfäl. Berggewerk-

[4] Girty (1918, p. 39) also lists "*Eumorphoceras bisulcatum?*" from the White Pine shale of southeastern California.

schaftskasse Bochum, p. 118; [part] ——, 1938, Geol. Jahresberichte, Bd. 1, p. 388; ?DEMANET, 1938, Mus. roy. Hist. nat. Belg., Mém., no. 84, pp. 115, 119, 177; ?——, 1938, Mus. roy. Hist. nat. Belg., Patrimoine, pp. 175, 245, pl. 130, figs. 6–9, and stratigraphic chart; ?HUDSON, 1939, Yorkshire Geol. Soc., n. ser., vol. 23, pp. 327, 329, 330, 332, 336, 337, 339; [part?] DEMANET, 1941, Mus. roy. Hist. nat. Belg., Mém. 97, pp. 15, 27, 29, 30, 32, 35–42, 47–49, 56–58, 137–140, 142, pl. 5, figs. 15–20; [part?] DELÉPINE, 1941, Protec. l'État français Maroc, Direct. gén. Trav. publics, Div. Mines et Géol., Serv. géol., Notes et Mém., No. 56, pp. 12, 20, 26, 32, 34, 37, 39–41, 79; MOORE, 1941, Yorkshire Geol. Soc., Proc., n. ser., vol. 24, pp. 253, 257; [part?] HUDSON and COTTON, 1943, Yorkshire Geol. Soc., Pr., n. ser., vol. 25, pp. 142, 145, 160–164, 167, 171; [part] SCHUCHERT, 1943, Stratigraphy of the eastern and central United States, p. 912 [not 852]; [part?] HUDSON, 1944, Leeds Philos. Soc., Pr., Sci. sect., vol. 4, pt. 3, pp. 233–241; [part] SHIMER and SHROCK, 1944, Index fossils of North America, p. 571, pl. 233, figs. 16–18; [part?] DUNHAM and STUBBLEFIELD, 1945, Quart. Jour. Geol. Soc. London, vol. 100, pp. 209, 212, 235, 238, 240, 258–260, pl. 11, figs. 4a–4c; [part?] HUDSON and COTTON, 1945, Quart. Jour. Geol. Soc. London, vol. 101, pp. 1, 2, 4–11, 13, 14; ?HUDSON, 1945, Quart. Jour. Geol. Soc. London, vol. 101, pp. 135–136; [part?] STUBBLEFIELD, 1945, Quart. Jour. Geol. Soc. London, vol. 101, pp. 136–137; ?HUDSON, 1945, Geol. Mag., vol. 82, no. 1, pp. 2, 3–4, 5; ?——, 1945, Yorkshire Geol. Soc., Proc., n. ser., vol. 25, pt. 4, pp. 318, 320; ?MOORE, 1945, Yorkshire Geol. Soc., Pr., n. ser., vol. 25, p. 333; [part?] MOORE, 1946, Yorkshire Geol. Soc., Pr., n. ser., vol. 25, pp. 388, 393, 394, 417, 430–433, 439, pl. 22, fig. 3; pl. 23, fig. 7; pl. 25, fig. 5; pl. 27, figs. 1, 2; ?JACKSON, 1946, Liverpool Geol. Soc., Pr., vol. 19, pt. 3, pp. 161, 162, 163, 164.

Three representatives of this species from the Barnett shale of Texas are illustrated. All of them are closely similar to the Caney syntypes figured by Girty and to similar conspecific specimens in our collections from the same formation. The largest of our specimens (pl. 100, figs. 13, 14) is about 11 mm. in diameter. It is septate throughout and therefore represents only phragmacone.

The general characters of the conch and the details of the ornamentation and the sutures are shown by the accompanying illustrations. The conch is subglobular and the whorls are distinctly wider than high. The lateral and dorsolateral zones of the conch bear small but prominent ribs, which curve orad and disappear ventrolaterally. There is a prominent longitudinal furrow or sulcus on each ventrolateral zone. In one of the small specimens (see pl. 100, fig. 15) the adapical portion of the outer volution bears a very distinct ventral groove. As shown by figure 17, this groove diminishes adorally and is entirely gone at the adoral end of the same volution. The growth lines form a deep more or less V-shaped but narrowly rounded ventral sinus. Each external suture forms a deep divided ventral lobe with strongly diverging flanks and on either side of it a rounded asymmetrically U-shaped first lateral saddle, a broadly V-shaped but very narrowly rounded first lateral lobe, a low broadly rounded second lateral saddle, and a shallow lobe that centers just inside the umbilical shoulder.

Remarks.—Girty (1911, pp. 103–104, pl. 16, fig. 4) referred to this species "a single specimen in a rather poor state of preservation" from the Ruddell shale of northeastern Arkansas (see pl. 100, fig. 8, of the present publication). He thought that this individual "probably represents a senile condition and exhibits such variations from the figured specimens of *E. bisulcatum* from the Caney shale as such a condition would naturally show." Miller and Furnish (1940, pp. 364, 365) placed this specimen with question in *Girtyoceras limatum* (Miller), the type specimens of which came from the Mississippian of central Kentucky; and Dunham and Stubblefield (1945, p. 258) accepted this identification. Dr. James Steele Williams of the U. S. Geological Survey has written us that this specimen "came from a nodule which when broken gave two impressions and a poor natural cast of the specimen. The better impression was used to make the squeeze that was figured" by Girty. Dr. Williams also kindly sent plaster casts of both the internal mold and the better half of the external mold, and these have convinced us that this specimen probably can not be differentiated specifically from typical *G. limatum*, though the constrictions on it are somewhat more numerous. It differs from *E. bisulcatum* in that it does not bear lateral ribs but instead has sinuous transverse constrictions that are confined to the umbilical half of the lateral zones of the conch, and its whorls are relatively narrow. Dr. G. A. Cooper of the U. S. National Museum loaned us for study two rather small testiferous

specimens which he collected from the Ruddell shale and which probably belong in *G. limatum*. They are very similar to equal-sized representatives of *G. meslerianum* (Girty) from the Caney shale of Oklahoma but they have a somewhat larger umbilicus, more pronounced growth lines, and smaller but more numerous constrictions—like typical small representatives of *G. meslerianum* of them are small and therefore probably immature, they come from beds that may not be contemporaneous with the Caney and the Barnett shales, and without an opportunity to make direct comparisons we are reluctant to express an opinion in regard to their affinities.

Occurrence.—Barnett formation at the following four localities in central Texas: (1)

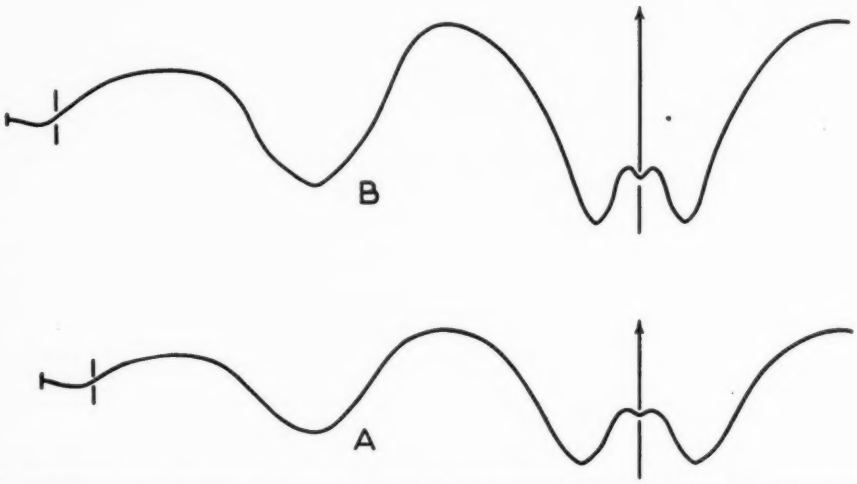


FIG. 2—*Eumorphoceras plummeri*, n. sp., (A), and *E. bisulcatum* Girty (B), both ×20. Diagrammatic representations of one of the adoral sutures of each of the specimens represented by figures 1–3 and 13, 14 on plate 100, at diameters of about 9 and 10 mm., respectively.

they do not bear a longitudinal groove or sulcus on each ventrolateral zone of the conch.

As indicated by the above synonymy, various paleontologists have referred to *Eumorphoceras bisulcatum* (including several varieties) specimens from numerous localities in Great Britain, Europe, and northern Africa. Some of these seem to resemble the American types rather closely. However, all

along San Saba-Bend road about 7 miles east of San Saba, San Saba County (pl. 100, figs. 9–12); (2) about 1900 feet due west from a point 1.93 miles south of the Honey Creek crossing of the Llano-Click road, which is about 15 miles by road southeast of Llano, Llano County (pl. 100, figs, 13, 14); (3) about 5000 feet N. 54°W. from the point where the county road from Mason to White's Crossing crosses Honey Creek, which

EXPLANATION OF PLATE 98

FIGS. *1–13*—*Goniatites choctawensis* Shumard. Figures *1–3*, an essentially complete specimen from the lower part of the Barnett formation (Bed 3 of Cloud and Barnes) about 10 miles southwest of Mason, Texas, ×1½. Figures *4*, *5*, a completely septate specimen from the Caney shale on the east side of Highway 48 in sec. 1, T. 2 N., R. 6 E., Pontotoc County, Oklahoma, ×1½. Figures *6–8*, a lirate specimen from the Barnett formation (Bed 9 of Cloud and Barnes) about 10 miles southwest of Mason, Texas, ×1. Figure *9*, a specimen from the same horizon and locality as figures *1–3*, ×1½. Figures *10*, *11*, a septate specimen from the upper part of the Barnett formation about 8 miles southwest of Mason, Texas, ×1½. Figures *12*, *13*, a rather poorly preserved specimen from the same horizon and locality as figures *1–3*, ×1½. (p. 658)

1

2

3

4

6

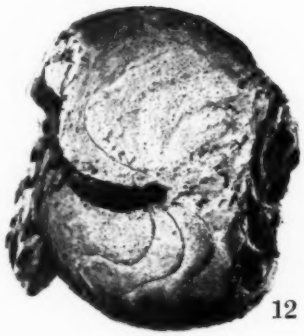
7

8

5

9

10


12

11

13

Miller and Youngquist, Mississippian Cephalopoda

Miller and Youngquist, Mississippian Cephalopoda

is about 8 miles by road southwest, of Mason, Mason County (pl. 100, figs. 15–17); and (4) south edge of borrow pit on south side of outcrop along San Saba-Chappel road some 2½ miles south-southeast of San Saba, San Saba County (1 unfigured specimen). The syntypes came from the Caney shale of southeastern Oklahoma, and in 1918 Girty listed this species with question from the White Pine shale of southeastern California. Bisat (1936, p. 531) stated that conspecific specimens occur in England, Scotland, Belgium, Holland, and Germany, an observation that we are not able to confirm or deny; and Delépine (1935, pp. 172, 184–185, pl. 8, figs. 5, 6) has illustrated and described a form from the French Pyrenees that is closely similar and possibly identical. Also, this latter author (Delépine, 1941, pp. 12, 79) has questionably referred a single small specimen from Morocco to this species.

Figured Specimens.—U. S. National Museum (pl. 100 figs. 13–17); and State University of Iowa, 6974 (pl. 100, figs. 9–12).

EUMORPHOCERAS PLUMMERI Miller and Youngquist, n. sp.

Plate 100, figures 1–4, 20, 21

Eumorphoceras bisulcatum [part?] BISAT, 1924, Yorkshire Geol. Soc., Pr., n. ser., vol. 20, pp. 72, 96–98, 99, 100, 117, pl. 6, figs. 1–5; pl. 10, fig. 12; [part?] SCHMIDT, 1925, Preuss. Geol. Landesanstalt, Jahrb., Bd. 45, pp. 497, 500, 501, 507, 511, 512, 530, 575, 577–579, 582–585, pl. 22, fig. 5; pl. 25, figs. 2, 3; [part?] BRAY, Manchester Geol. Assoc., Jour., vol. 1, pt. 1, p. 54; [part?] BISAT, 1928, C. R. Cong. l'avanc. études Stratigr. Carbon. Heerlen, 1927, pp. 127, 132, pl. 6; ?MAILLIEUX and DEMANET, 1929, Soc. Belge Géol., Bull., t. 38, p. 129, tab. 1; [part?] SCHMIDT, 1929, Tierische Leitfossilien des Karbon, Gürich's Leitfossilien, Lief. 6, pp. 70–71, pl. 19, figs. 5, 6; [part?] BISAT, 1930, Leeds Geol. Assoc., Tr., pt. 20, p. 31; [part?] DELÉPINE, 1930, Inst. géol. Univ. Louvain, Mém., t. 6, fasc. 1, pp. 57–58, 62, 63, pl. 1, figs. 1–5; ?MOORE, 1930, Manchester Geol. Assoc., Jour., vol. 1, pp. 106, 107, 108; ?BISAT, 1931, Leeds Geol. Assoc., Tr., vol. 5, pp. 27, 30; [part?] DELÉPINE, 1931, C. R. Cong. Soc. Savantes, 1928, Lille, p. 135; [part] MAILLIEUX, 1933, Mus. royal Hist. nat. Belg., Partrimoine, pp. 100, 102, pl. 10, fig. 139; [part?] BISAT, 1933, Geol. Assoc. Proc., vol. 44, pt. 3, p. 256, pl. 30; VERHOOGEN, 1934, Soc. Géol. Belg., Ann., t. 58, Bull. 2, pp. B98, B99; [part?] SCHMIDT, 1934, Preuss. Geol. Landesanstalt, Jahrb., Bd. 54, pp. 442–451, 454, 455, 459, 460, 461; ?BISAT, 1934, Leeds Geol. Assoc., Trans., vol. 5, pt. 2, pp. 115–117; ?HUDSON, 1934, Leeds Geol. Assoc., Trans., vol. 5, pt. 2, pp. 119, 120, 121, 122, 123; ?WOOD, 1936, Liverpool Geol. Soc., Pr., vol. 17, pt. 1, pp. 16, 17, 23; [part?] BISAT, 1936, Internat. Geol. Cong., Rept. 16th sess., vol. 1, pp. 531, 534, table 1; [part] PLUMMER and SCOTT, 1937, Texas Univ. Bull. 3701, pp. 15, 16, 175–176, 378, 382, 383, 384, 399, 401, pl. 38, figs. 4–6 [not 7]; [part?] HUDSON and MITCHELL, 1937, Geol. Surv., Summ. Prog. for 1935, pt. 2, p. 5; [part?] HUDSON, 1938, Geol. Assoc., Proc., vol. 49, pt. 3, pp. 316, 321–322; [part?] HUDSON, 1938, Geol. Assoc., Proc., vol. 49, pt. 4, p. 357; [part?] HUDSON and EDWARDS, 1938, Geol. Assoc., Proc., vol. 49, pt. 4, pp. 358, 362, 363, 371; [part?] SCHMIDT, 1938, Geol. niederrheinisch-westfälischen Steinkohlengebietes im auftrage westfäl. Bergewerkschaftskasse Bochum, p. 118; [part] ———, 1938, Geol. Jahresberichte, Bd. 1, p. 388; ?DEMANET, 1938, Mus. royal Hist. nat. Belg., Mém., No. 84, pp. 115, 119, 177; ?———, 1938, Mus. royal Hist. nat. Belg., Patrimoine, pp. 175, 245, pl. 130, figs. 6–9, and stratigraphic chart; ?HUDSON, 1939, Yorkshire Geol. Soc., n. ser., vol. 23, pp. 327, 329, 330, 332, 336, 337, 339; [part?] DEMANET, 1941, Mus. royal Hist. nat. Belgium, Mém. 97, pp. 15, 27, 29, 30, 32, 35, 36, 37, 38, 39, 40, 41, 42, 47–48, 49, 56, 57, 58, 137–140, 142, pl. 5, figs. 15–20; [part?] DELÉPINE, 1941, Protec. l'État français Maroc, Direct. gén. Trav. publics, Div. Mines et géol., Serv. géol., Notes et Mém., No. 56, pp. 12, 20, 26, 32, 34, 37, 39–41, 79; [part?], HUDSON and COTTON, 1943, Yorkshire Geol. Soc., Proc., n. ser., vol. 25, pp. 142, 145, 160, 161, 162, 163, 164, 167, 171; [part] SCHUCHERT, 1943, Stratigraphy of the eastern and central United States, p. 912, [not 852]; [part?] HUDSON, 1944, Leeds Philos. Soc., Proc., Sci. sect., vol. 4, pt. 3, pp. 233–241; [part] SHIMER and SHROCK, 1944, Index fossils of North America, p. 571, pl. 233, figs. 16–18; [part?] DUNHAM and STUBBLEFIELD, 1945, Quart. Jour. Geol. Soc. London, vol. 100, pp. 209, 212, 235, 238, 240, 258–260, pl. 11, figs. 4a–4c; [part?] HUDSON and COTTON, 1945,

---

EXPLANATION OF PLATE 99

All specimens are from the Barnett shale about 2½ miles southeast of San Saba, Texas.

FIGS. *1–19—Goniatites choctawensis* Shumard. Figures *1, 2*, a globose specimen, ×1½. Figures *3–5*, a small specimen, ×2. Figures *6, 7*, another small specimen, ×2. Figures *8, 9*, a fragmentary specimen, ×2. Figures *10–12*, an immature specimen, ×3. Figures *13–15*, a septate individual, ×1½. Figures *16–19*, a large specimen, the holotype of *Goniatites choctawensis barnettensis*, n. var., ×1.

(p. 658)

Quart. Jour. Geol. Soc. London, vol. 101, pp. 1, 2, 4, 7–11, 13, 14; ?HUDSON, 1945, Quart. Jour. Geol. Soc. London, vol. 101, pp. 135–136; [part?] STUBBLEFIELD, 1945, Quart. Jour. Geol. Soc. London, vol. 101, pp. 136–137; ?HUDSON, 1945, Geol. Mag., vol. 82, no. 1, pp. 2–5; ?———, 1945, Yorkshire Geol. Soc., Proc., n. ser., vol. 25, pt. 4, pp. 318, 320; [part?] MOORE, 1946, Yorkshire Geol. Soc., Proc., n. ser., vol. 25, pp. 388, 393, 394, 417, 430–433, 439, pl. 22, fig. 3; pl. 23, fig. 7; pl. 25, fig. 5; pl. 27, figs. 1, 2; ?JACKSON, 1946, Liverpool Geol. Soc., Pr., vol. 19, pt. 3, pp. 161, 162, 163, 164.

We are basing this species primarily on three specimens, all of which are illustrated. The best of these, an almost complete internal mold, (pl. 100, figs. 1–3) is designated the holotype. The adoral three-fifths of its outer volution is non-septate and presumably represents the living chamber. All of the preserved part of the outer volution of the paratype represented by figure 4 and about three-fifths of the adoral volution of that represented by figures 20 and 21 are also non-septate.

The maximum diameter of the holotype is about 14 mm., and slightly apicad of its adoral end its conch is about 5½ mm. high and 5 mm. (estimated) wide. The specimen is discoidal in shape, and the whorls, though impressed dorsally, are otherwise subrectangular in cross section for they are considerably flattened both laterally and ventrally and are abruptly rounded both ventrolaterally and dorsolaterally. The paratype represented by figures 20 and 21 shows that the conch of this species attained a maximum diameter of at least 20 mm.; slightly apicad of the adoral end, this specimen is about 9 mm. high and 6½ mm. wide.

The umbilicus is moderate in size, and its diameter is about a fifth that of the specimen. The maximum diameter of the umbilicus of the holotype is about 3 mm. The umbilical shoulders are abrupt, and the umbilical walls are steep and approximately normal to the flattened lateral zones of the conch.

Fragments that adhere to the adoral portion of the holotype show that the test is thin, and that on its surface there are numerous fine growth lines. These form a deep U-shaped ventral sinus and on either side of it a high very narrowly rounded ventrolateral salient, a broadly rounded lateral sinus, and a dorsolateral salient. On the dorsolateral and lateral zones of the conch there are small but prominent sinuous ribs parallel to the growth lines. There are about 20 of these ribs on the outer volution of the holotype. Dorsally they end very abruptly on the umbilical shoulders. Ventrally they more or less diffuse into the growth lines, suggesting that they represent fasciculate growth lines. Slightly dorsad of each ventrolateral shoulder there is a prominent longitudinal groove or sulcus. Along the venter of the internal mold there is a faint but clearly discernible line.

Each external suture forms a broad rather prominently divided ventral lobe and on either side of it an asymmetrical depressed-U-shaped first lateral saddle, a depressed-V-shaped but narrowly rounded first lateral lobe, a low broadly rounded second lateral saddle, and a slight lobe on the umbilical wall (see text figure 2A).

Remarks.—All three of the type specimens of this species are strikingly similar to each other and to the specimen from the same general zone and locality that was figured by Plummer and Scott (1937, pl. 38, figs. 4, 5). Also they appear to resemble very closely the form that Moore (1946, pl. 22, fig. 3) recently illustrated from the "Sabden Shales, near Samlesbury Bottoms, River Darwen, Lancashire; *N.* [*Nuculoceras*] *nuculum* subzone, Arnsbergian (E_2), Namurian." We are uncertain as to the relationship of our new species to varieties of *E. bisulcatum* Girty that have been proposed by several European paleontologists.

Mature representatives of this species differ from those of *Eumorphoceras bisulcatum*, with which they are directly associated, in that their conchs are compressed, higher than wide, and flattened ventrally, and their sutures less strongly sinuous. Presumably early growth stages of these two species are almost identical, and the small specimens illustrated by figures 9–12, 15–17, on plate 100 may be immature representatives of this species rather than of *E. bisulcatum*.

The specific name is given in honor of the late Professor F. B. Plummer, who contributed greatly to our knowledge of Texas Paleozoic ammonoids.

Occurrence.—Barnett formation at the

following three localities in central Texas: (1) borrow pit on south side of outcrop along San Saba-Chappel road some 2½ miles south-southeast of San Saba, San Saba County (pl. 7, figs. 1–3); (2) along San Saba-Bend road about 7 miles east of San Saba, San Saba County (pl. 7, fig. 4); and (3) about 5000 feet N. 54°W. from the point where the county road from Mason to White's Crossing crosses Honey Creek, which itself is about 8 miles by road southwest of Mason, Mason County (pl. 7, figs. 20, 21). Also, as indicated above, the Sabden shales of northwestern England carry a form that is closely similar and may be conspecific.

Types.—U. S. National Museum (pl. 100, figs. 1–3—holotype; figs. 20, 21—paratype); and State University of Iowa, 6975 (pl. 100, fig. 4—paratype).

GIRTYOCERAS MESLERIANUM (Girty)
Plate 94, figures 10, 11; plate 100, figures 22–24

Adelphoceras meslerianum GIRTY, 1909, U. S. Geol. Survey Bull. 377, pp. 10, 66–67, pl. 12, figs. 1–2a [not 3–3c]; WEDEKIND, 1914, Mitt. Mus. Stadt Essen, Heft 1, p. 11; MORGAN, 1924, [Oklahoma] Bur. Geol. Bull. 2, p. 54; BISAT, 1924, The Naturalist, p. 87; ?CRONEIS, 1930, Arkansas Geol. Surv. Bull. 3, pp. 56, 65; PLUMMER and SCOTT, 1937, Texas Univ. Bull. 3701, p. 174, pl. 38, figs. 17, 18; SCHUCHERT, 1943, Stratigraphy of the eastern and central United States, p. 852.

Girtyoceras meslerianum WEDEKIND, 1918, Palaeontographica, Bd. 62, p. 140; ?BRÜNING, 1923, Geol. Archiv, Bd. 1, Heft 5, p. 265 [see *Homoceras brüningianum* Schmidt (1925, p. 580)]; MILLER, 1934, Am. Jour. Sci., 5th ser., vol. 28, p. 33; ——— and FURNISH, 1940, Jour. Paleontology, vol. 14, pp. 356, 363–364, 365, 367–368, pl. 48, figs. 1–3; LIBROVITCH, 1940, Acad. Sci. USSR, Paleont. Inst., Paleontology of USSR, vol. 4, pt. 9, fasc. 1, pp. 310–311; MOORE, 1941, Yorkshire Geol. Soc., Pr., n. ser., vol. 24, p. 253; SHIMER and SHROCK, 1944, Index fossils of North America, p. 571; HUDSON and COTTON, 1945, Yorkshire Geol. Soc., Pr., n. ser., vol. 25, pp. 256, 260, 262, 271, 276; MOORE, 1946, Yorkshire Geol. Soc., Pr., n. ser., vol. 25, pp. 389, 390, 393, 395, 397, 401, 402, 403, 405, 407, 413, 415, 440, pl. 23, figs. 3–6.

Beyrichoceras meslerianum BISAT, 1924, Yorkshire Geol. Soc., Pr., n. ser., vol. 20, pp. 72, 82.

Dryochoceras brainerdi [and "*grainerdi*"] MORGAN, 1924, [Oklahoma] Bur. Geol. Bull. 2, pp. 185–186, pl. 52, figs. 7–7b.

Homoceras meslerianum [part?] SCHMIDT, 1923, Centralblatt f. Min., etc., Jahrg. 1923, no. 24, p. 745; [part?] ———, 1925, Preuss. Geol. Landesanstalt, Jahrb., Bd. 45, pp. 496, 499, 500, 508, 511, 530, 574, 576, 580, 581, pl. 21, fig. 18; pl. 24, figs. 24–26.

Histrioceras meslerianum [part?] SCHMIDT, 1923, Centralblatt f. Min., etc., Jahrg. 1923, no. 24, p. 745.

Sagittoceras meslerianum BISAT, 1928, C. R. Cong. l'avanc. études Stratigr. Carbon., Heerlen, 1927, p. 125; [part?] SCHMIDT, 1929, Tierische Leitfossilien des Karbon, Gürich's Leitfossilien, Lief. 6, p. 69, pl. 18, figs. 20–22; ?BISAT, 1930, Leeds Geol. Assoc., Tr., pt. 20, p. 31; KOBOLD, 1933, Preuss. Geol. Landesanstalt, Jahrb., Bd. 53, pp. 477, 482, 505–506; BISAT, 1933, Geol. Assoc., Pr., vol. 44, p. 256; ———, 1936, Internat. Geol. Cong. Rept. 16th sess., vol. 1, pp. 531, 533; [part?] MOORE, 1936, Manchester Geol. Assoc., Jour., vol. 1, pp. 177, 178, fig. 2; [part?] HUDSON and MITCHELL, 1937, Geol. Surv., Summ. Prog. for 1935, pp. 25, 26; HUDSON, 1938, Geol. Assoc., Pr., vol. 49, pt. 3, p. 315; ?——— and COTTON, 1943, Yorkshire Geol. Soc., Pr., n. ser., vol. 25, p. 170.

Sagittoceras brainerdi MILLER, 1934, Am. Jour. Sci., 5th ser., vol. 28, pp. 31, 32; MOORE, 1936, Manchester Geol. Assoc., Jour., vol. 1, p. 177.

Our extensive collections from the Barnett contain only one specimen that we can definitely refer to this species. It is, however, an exceptionally fine large specimen, which is septate throughout.

The conch is sublenticular and the whorls are compressed, flattened laterally (with the lateral zones converging ventrad), and angular ventrally. The maximum diameter of the specimen measures about 73 mm. Near its adoral end, the maximum height and width of the conch are about 43 mm. and 23 mm., respectively; and corresponding measurements near the mid-length of the outer volution are about 24 mm. and 15 mm. These figures make it clear that the conch is expanded orad rather rapidly.

The umbilicus is rather small but deep, and the umbilical shoulders are rounded. The maximum diameter of the umbilicus is about 8 mm.

The test is thin and bears numerous fine growth lines each of which forms a rather deep V-shaped ventral sinus. Also, there is a faint longitudinal groove some 2 or 3 mm. wide on each lateral zone about a third of the distance from the venter to the umbilical shoulder. In the outer volution (the only one visible) there are no transverse constrictions.

The camerae are short and the sutures overlap greatly. Each suture forms a large deep ventral lobe (that is divided by a high secondary saddle which is itself divided by

a rather prominent narrow median lobe) and on either side of it a high asymmetrically V-shaped first lateral saddle, a shorter acuminate first lateral lobe, and a broadly rounded saddle that extends to the umbilicus. The flanks (secondary lobes) of the ventral lobe are rather narrowly V-shaped and sharply pointed. The adjacent saddles in the ventral lobe are U-shaped.

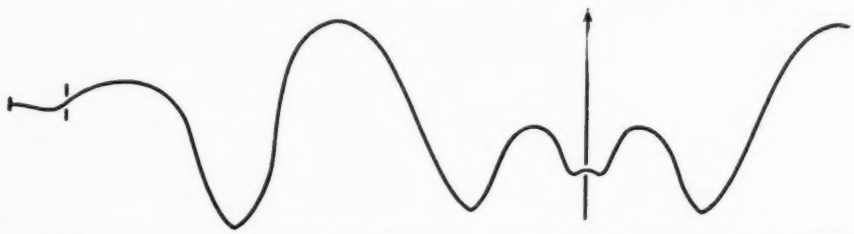


FIG. 3—*Girtyoceras ornatissimum*, n. sp., ×10. Diagrammatic representation of the adoral suture of the holotype, which is about 14 mm. in diameter.

Remarks.—This specimen is closely similar to one from the Caney shale near Ada, Oklahoma, illustrated and described by Morgan as *Dryochoceras brainerdi*. As noted by Miller and Furnish (1940, pp. 363–364), it now seems almost certain that Morgan's specimen is merely a large representative of *Girtyoceras meslerianum*, and by analogy our specimen is also referable to that species.

These two large specimens resemble mature representatives of the genotype of *Gonioglyphioceras, G. gracile* (Girty) of the Pennsylvanian Boggy and Wewoka formations of Oklahoma. However, in that species the conch is retuse ventrally. Both Elias (1934, p. 92) and Miller and Furnish (1940, p. 364) have indicated that the peripheral groove is confined to the test and that the internal mold is not divided ventrally. However, the John Britts Owen collection, which is now at the State University of Iowa, contains two moderately large representatives of *G. gracile*, in both of which there is a ventral furrow on the internal mold.

Small representatives of *Girtyoceras meslerianum* bear prominent sinuous transverse constrictions (pl. 100, figs. 22–24). However, in later growth stages these become obsolete and eventually disappear.

Ocurrence.—Upper part of Barnett formation about 5000 feet N. 54°W. from the point where the county road from Mason to White's Crossing crosses Honey Creek, which itself is about 8 miles by road southwest of Mason, Mason County, Texas. The type specimens of this species came from the Caney shale of Oklahoma, and conspecific specimens have been illustrated from

---

EXPLANATION OF PLATE 100

FIGS. *1–4—Eumorphoceras plummeri*, n. sp. The holotype (figs. *1–3*) and one of the paratypes (fig. *4*), both ×2. From the Barnett shale about 2½ miles south-southeast of San Saba, Texas (holotype) and 7 miles east of the same city (paratype). (p. 665)

5–7—Girtyoceras ornatissimum, n. sp. The holotype, from the Barnett shale about 2½ miles south-southeast of San Saba, Texas, ×2. (p. 669)

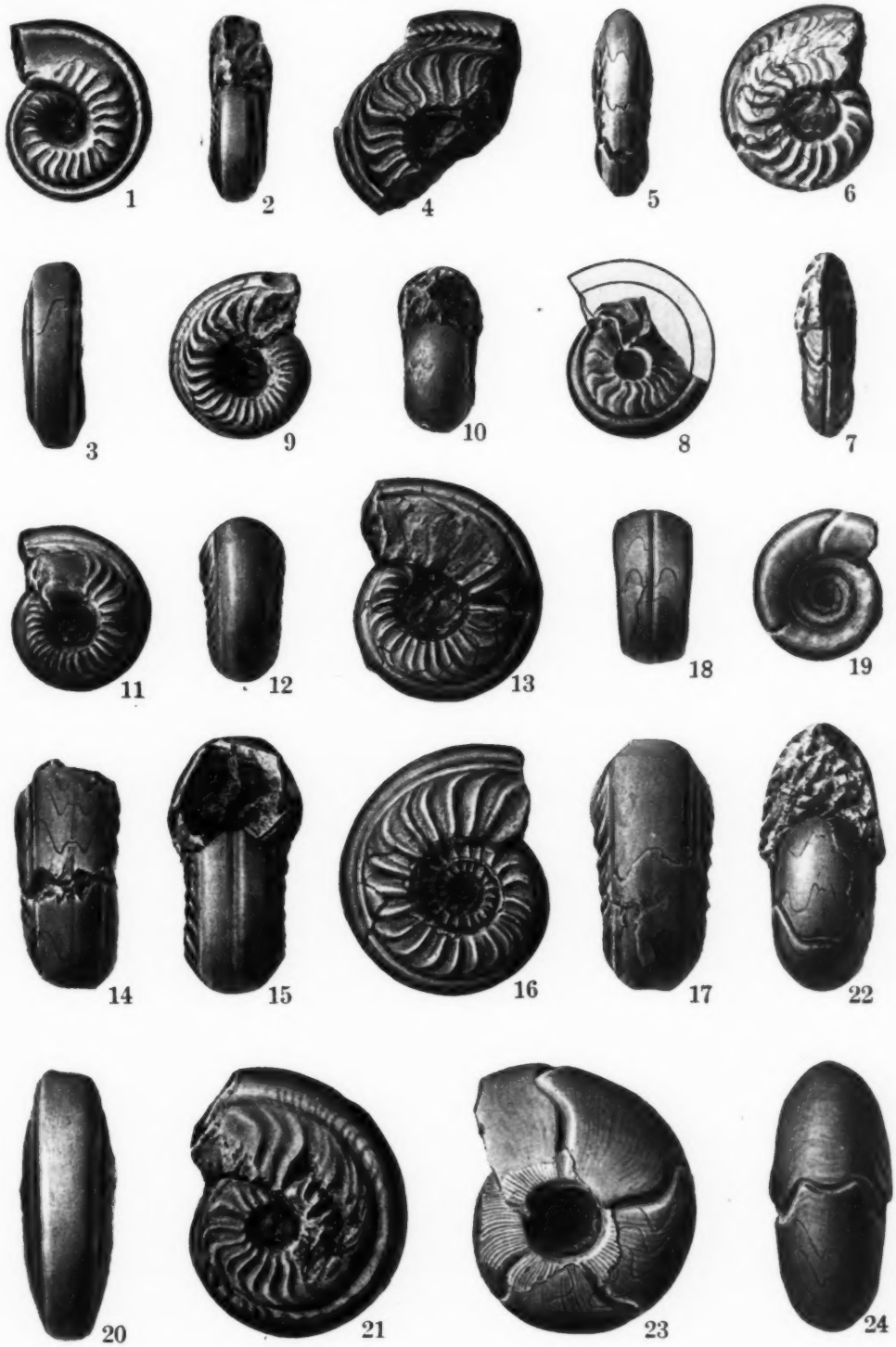
8—Girtyoceras limatum (Miller)? An artificial cast of a specimen from the Ruddell shale at Howards Wells, Independence County, Arkansas, ×1. After Girty. (p. 663)

9–17—Eumorphoceras bisulcatum Girty. Figures *9–12*, a small specimen from the Barnett shale about 7 miles east of San Saba, Texas, ×4. Figures *13, 14*, a specimen from the same formation about 15 miles southeast of Llano, Texas, ×3. Figures *15–17*, a small specimen from the upper part of the Barnett about 8 miles southwest of Mason, Texas, ×5. (p. 662)

18, 19—Cravenoceras nevadense Miller and Furnish. A small specimen from the Barnett shale about 2½ miles southeast of San Saba, Texas, ×4. (p. 657)

20, 21—Eumorphoceras plummeri, n. sp. One of the paratypes, from the upper part of the Barnet shale about 8 miles southwest of Mason, Texas, ×2. (p. 665)

22–24—Girtyoceras meslerianum (Girty). A well preserved specimen from the Caney shale on the east side of Highway 48 in sec. 1, T. 2 N., R. 6 E., Pontotoc County, Oklahoma, ×3. (p. 667)



Miller and Youngquist, Mississippian Cephalopoda

the Floyd shale of Georgia. Also, this species is stated to occur in the upper Viséan at various localities in western Europe and England.

Figured Specimens.—U. S. National Museum (pl. 94, figs. 10, 11); and State University of Iowa, 6976 (pl. 100, figs. 22–24)

GIRTYOCERAS ORNATISSIMUM, Miller and Youngquist, n. sp.
Plate 100, figures 5–7

The Barnett shale has yielded a unique specimen that apparently represents a new species. It is a well preserved internal mold that is completely septate. This individual is small and sublenticular as the adoral portion of its conch is compressed, flattened laterally and narrowly rounded ventrally. The maximum diameter is about 14 mm., and near its adoral end the conch is about 6½ mm. high and 4½ mm. wide. Near the adapical end of the outer volution, the height and width of conch measure about 2½ mm. and 3½ mm., respectively. The adapical portion of the outer volution of this specimen is depressed dorsoventrally whereas the adoral portion is compressed laterally.

The umbilicus is moderately large, and the maximum diameter attained by it in the holotype is slightly more than 4 mm. The umbilical shoulders are abruptly rounded, and the umbilical walls are steep and essentially normal to the flattened lateral zones of the conch.

Traces of the growth increments on this specimen form a deep U-shaped ventral sinus and on either side of it a high more or less V-shaped asymmetrical ventrolateral salient and a broadly rounded asymmetrical lateral sinus. On the ventrolateral and lateral zones they merge with rather prominent ribs, which are largely confined to the lateral zones of the whorls. The ribs end abruptly at the umbilical shoulders, but on the ventrolateral zones they seem to diffuse into the growth increments. Between certain of the ribs there are sinuous transverse constrictions which parallel the increments of growth. There are at least five constrictions in the outer volution. They are particularly prominent in the adapical portion of this volution, where they are relatively far apart and continue across the venter. Also, there is a longitudinal groove or sulcus on each ventrolateral zone and in the adapical portion of the outer volution there is a groove along the venter.

In the adoral portion of this specimen each external suture consists of a rather low very broad prominently divided ventral lobe and on either side of it a rounded asymmetrical U-shaped first lateral saddle, a V-shaped asymmetrical pointed first lateral lobe (which is deeper than the ventral lobe), a relatively low broadly rounded second lateral saddle, and a shallow rounded lobe on the umbilical wall.

Remarks.—In the outer volution, the holotype changes greatly in shape, ornamentation, and sutures, suggesting that the preserved part of the conch is largely (if not entirely) immature. The prominent ribs and ventrolateral sulci suggest a relationship to *Eumorphoceras*, whereas the narrowly rounded venter, the transverse constrictions, the rapid adoral decrease in the prominence of the ribs, and the angularity of the lobes of the adoral sutures all suggest an affinity with *Girtyoceras*. Thus it seems that this form is more or less intermediate between typical *Eumorphoceras* and typical *Girtyoceras*, but it is closer to the latter.

Occurrence.—Barnett formation near borrow pit on south side of outcrop along San Saba-Chappel road some 2½ miles south-southeast of San Saba, San Saba County, Texas.

Holotype—U. S. National Museum.

APPENDIX

CRAVENOCERAS FROM THE PITKIN LIMESTONE OF ARKANSAS
Plate 95, figure, 1–3

Easton (1942, pl. 12, figs. 2–4) figured an ammonoid from the Pitkin limestone of northern Arkansas, which is the uppermost Mississippian formation in that region and is generally regarded as Chester in age. This specimen, which has been available for study does not reveal the nature of the sutures. However, its general form, the size and shape of the umbilicus, and the nature of the surface markings all indicate that it belongs in the genus *Cravenoceras*, and that it is closely related to (if not identical with). *C. hesperium* Miller and Furnish of the White Pine

shale of Nevada and probably the Barnett formation of central Texas.

This specimen is preserved in buff-colored fine-grained limestone which retains the details of the surface ornamentation. Since no sutures are visible, the outer whorl is believed to represent the living chamber. The diameter of the specimen is about 20 mm.; the maximum height and width of conch measure about 11 mm. and 17 mm., respectively; and the umbilicus attains a diameter of about 3½ mm. The umbilical walls are steep and almost normal to the lateral zones. The internal mold, but apparently not the test, bears sinuous transverse constrictions, of which there appear to be three in the outer volution. The growth lines, which are fairly prominent and slightly sinuous, form a slight ventral sinus that is located in the center of a somewhat more prominent broad ventral salient; on each side of the conch the growth lines form a broad shallow rounded ventrolateral sinus and a similar lateral salient. Traces of these growth lines are clearly visible on the internal mold, where they are essentially parallel to the constrictions.

Dr. James Steele Williams of the U. S. Geological Survey has written us that this specimen came from the basal 5 feet of the Pitkin limestone at Pilot Mountain, 3 miles east of Saint Joe, Searey County, north-central Arkansas. It is in the "Girty Collection" in the U. S. National Museum, where it bears the number 1487/E, blue.

REFERENCES

BISAT, W. S., 1924, The Carboniferous goniatites of the north of England and their zones: Yorkshire Geol. Soc., Pr., n. ser., vol. 20, pp. 40–124, pls. 1–10.

——, 1928, The Carboniferous goniatite zones of England and their continental equivalents: C. R. Cong. l'avanc. étud. Stratigr. Carbon, Heerlen, 1927, pp. 117–133, pls. 6, 6A.

——, 1936, The faunal stratigraphy and goniatite phylogeny of the Carboniferous of western Europe, with notes on the connecting links with North America: Internat. Geol. Cong., Rept. 16th sess., vol. 1, pp. 529–537, 1 pl.

CLOUD, P. E., JR., and BARNES, V. E., 1948, The Ellenburger group of central Texas: Texas Univ. Bull. (in press).

DELÉPINE, G., 1935, Contribution a l'étude de la faune du Dinantien des Pyrénées: Soc. géol. France, Bull., 5e sér., t. 5, pp. 65–75, 171–191, pls. 1, 7, 8.

——, 1941, Les goniatites du Carbonifère du Maroc et des confins Algéro-Marocains du Sud (Dinantien-Westphalien): Protect. l'État Français au Maroc, Direct. gén. Trav. Pub., Div. Mines et Géol., Serv. Géol., Notes et Mém., no. 56, pp. 1–110, pls. 1–8.

DUNHAM, K. C., and STUBBLEFIELD, C. J., 1945, The stratigraphy, structure and mineralization of the Greenhow mining area, Yorkshire: Quart. Jour. Geol. Soc. London, vol. 100, pp. 209–268, pls. 11, 12.

EASTON, W. H., 1942, Pitkin limestone of northern Arkansas: Arkansas Geol. Surv. Bull. 8, pp. 1–115, pls. 1–12.

ELIAS, M. K., 1938, Studies of late Paleozoic ammonoids: Jour. Paleontology, vol. 12, pp. 86–105, pls. 19, 20.

GABB, W. M., 1861, Descriptions of new species of American Tertiary fossils and a new Carboniferous cephalopod from Texas: Philadelphia Acad. Nat. Sci., Pr. 1861, pp. 367–372.

GIRTY, G. H., 1909, The fauna of the Caney shale of Oklahoma: U. S. Geol. Survey Bull. 377, pp. 1–106, pls. 1–13.

——, 1911, The fauna of the Moorefield shale of Arkansas: U. S. Geol. Survey Bull. 439, pp. 1–148, pls. 1–15.

——, 1915, The fauna of the Batesville sandstone of northern Arkansas: U. S. Geol. Survey Bull. 593, pp. 1–170, pls. 1–11.

——, 1918, *see* KNOPF, ADOLPH, and KIRK, EDWIN.

——, 1919, The Bend formation and its correlation: Am. Assoc. Petroleum Geol., Bull., vol. 3, pp. 71–81.

——, 1926, *see* ROUNDY, P. V., GIRTY, G. H., and GOLDMAN, M. I.

——, 1934, *see* KING, P. B.

GORDON, MACKENZIE, JR., 1944, Moorefield formation and Ruddell shale, Batesville district, Arkansas: Am. Assoc. Petroleum Geol., Bull., vol. 28, pp. 1626–1634.

HALL, JAMES, and WHITFIELD, R. P., 1877, Paleontology, U. S. Geol. Explor. Fortieth Parallel (King), vol. 4, pp. 197–302, pls. 1–7.

HIND, WHEELTON, 1918, On the distribution of the British Carboniferous goniatites, with a description of one new genus and some new species: Geol. Mag., dec. 6, vol. 5, pp. 434–450, pl. 16.

HYATT, ALPHEUS, 1883–1884, Genera of fossil cephalopods: Boston Soc. Nat. Hist., Pr., vol. 22, pp. 253–338 [pp. 253–272 were published in Dec. 1883, pp. 273–338 in Jan. 1884].

——, 1893, Carboniferous cephalopods; Second paper: Texas Geol. Surv., Ann. Rept. 4, pp. 377–474.

KING, P. B., 1934, Notes on upper Mississippian rocks in trans-Pecos Texas: Am. Assoc. Petroleum Geol., Bull., vol. 18, pp. 1537–1543.

KNOPF, ADOLPH, and KIRK, EDWIN, 1918, A geologic reconnaissance of the Inyo Range and the eastern slope of the southern Sierra Nevada, California (by Adolph Knopf) with a section on the stratigraphy of the Inyo Range (by Edwin Kirk): U. S. Geol. Surv. Prof. Paper 110, pp. 1–130, pls. 1–23.

LIBROVITCH, L. S., 1940, Carboniferous ammonoids of north Kazakhstan: Acad. Sci. USSR, Paleont. Inst., Paleont. USSR, vol. 4, pt. 9, fasc. 1, pp. 1–395, pls. 1–25.

MILLER, A. K., and FURNISH, W. M., 1940, Studies of Carboniferous ammonoids, Parts 1–4: Jour. Paleontology, vol. 14, pp. 356–377, pls. 45–49.

MOORE, E. W. J., 1946, The Carboniferous goniatite genera *Girtyoceras* and *Eumorphoceras:* Yorkshire Geol. Soc., Pr., vol. 25, pp. 387–445, pls. 22–27.

PHILLIPS, JOHN, 1836, Illustrations of the geology of Yorkshire . . . , Part II, The Mountain limestone district, pp. 1–253, pls. 1–25.

PLUMMER, F. B., and MOORE, R. C., 1922 [1921], Stratigraphy of the Pennsylvanian formations of north-central Texas: Texas Univ. Bull. 2132, pp. 1–237, pls. 1–27.

——, and SCOTT, GAYLE, 1937, Upper Paleozoic ammonites in Texas: Texas Univ. Bull. 3701, pp. 1–516, pls. 1–41.

——, ——, 1938, New Pennsylvanian ammonoid fauna from the Millsap Lake formation (Strawn group) of Texas (Abstract): Geol. Soc. Am., Bull., vol. 49, pp. 1919–1920.

ROUNDY, P. V., GIRTY, G. H., and GOLDMAN, M. I., 1926, Mississippian formations of San Saba County, Texas: U. S. Geol. Survey Prof. Paper 146, pp. 1–59, pls. 1–33.

SCHMIDT, HERMANN, 1925, Die carbonischen Goniatiten Deutschlands: Preuss. geol. Landesanstalt, Jahrb., Bd. 45, pp. 489–609, pls. 19–26.

SHUMARD, B. F., 1863, Descriptions of new Palaeozoic fossils: St. Louis Acad. Sci., Tr., vol. 2, pp. 108–113.

SMITH, J. P., 1903, The Carboniferous ammonoids of America: U. S. Geol. Surv. Mon. 42, pp. 1–211, pls. 1–29.

JOURNAL OF PALEONTOLOGY, VOL. 22, NO. 6, PP. 672–680, PLS. 101–103, 3 TEXT FIGS., NOVEMBER 1948

A CEPHALOPOD FAUNA FROM THE TYPE SECTION OF THE PENNSYLVANIAN "WINSLOW FORMATION" OF ARKANSAS

A. K. MILLER AND R. H. DOWNS
State University of Iowa, Iowa City, Iowa
(WITH NOTES ON THE LOCATION AND STRATIGRAPHIC RELATIONS BY LLOYD G. HENBEST, U. S. GEOLOGICAL SURVEY, WASHINGTON, D. C.)

ABSTRACT—Representatives of the following genera are described from the early Middle Pennsylvanian strata at Winslow in northwestern Arkansas: *Mooreoceras*, *Knightoceras*, *Pseudoparalegoceras*, and a new genus for which the name *Winslowoceras* is proposed. It is concluded that the beds which yielded these nautiloids and ammonoids are the approximate correlative of the Atoka formation of south-central Oklahoma. Included as an appendix is a discussion of some specimens of *Gastrioceras branneri branneri* Smith from the Lower Pennsylvanian Hale formation at a near-by locality.

THROUGH the courtesy of Messrs. Lloyd G. Henbest and James Steele Williams of the United States Geological Survey, some 25 nautiloids and 75 ammonoids from the early Middle Pennsylvanian strata exposed at Winslow, Arkansas, were recently sent to us for study. These specimens are particularly significant for they are the first cephalopods to be recorded from this locality, they are large and well preserved, and they represent four generic types, one of which has not been recognized previously.

The fossiliferous beds at Winslow constitute the basal portion of the old "Winslow formation." In her well known *Lexicon of geologic names of the United States*, Wilmarth pointed out that, as had long been recognized, this name was applied to rocks that may be subdivided into several formations. That is, in the Winslow area it embraced the Atoka formation, the Hartshorne sandstone, and the lower part of the McAlester formation; and as used in some other areas it included, in addition, the upper part of the McAlester formation, the overlying Savanna sandstone, and at least the lower part of the Boggy shale. "This blanket name has therefore been discarded."

However, in the opinion of some geologists, it may have been a mistake to abandon this term, because the beds at Winslow, though named later than the Atoka formation, are not involved in a complicated structure and can be fitted with more certainty into the unparalleled section of late Paleozoic strata that is exposed from the Ozark uplift to central Kansas by way of Arkansas. Therefore, we are retaining the old name, but to call attention to its dubious status, we are placing it in quotation marks.

The one abundant ammonoid in the assemblage under consideration, *Pseudoparalegoceras williamsi*, is strikingly similar to and is almost certainly conspecific with numerous specimens in the collections available to us from typical Atoka sandstone north of Clarita, in south-central Oklahoma. Accordingly, there is little doubt in our mind that the cephalopod-bearing beds in these two areas, about 160 miles apart, are

EXPLANATION OF PLATE 101

The illustrated specimens are from a thin brown ferruginous sandstone bed about 125–150 feet above the base of the "Winslow formation" at its type locality on the eastern side of a ditch about 430 feet north of the north portal of the Saint Louis-San Francisco Railroad tunnel at Winslow, Washington County, Arkansas. They are deposited in the U. S. National Museum.

FIGS. *1–4*—*Knightoceras oxylobatum* Miller and Downs, n. sp. The holotype, ×1 (figs. *1–3*) and ×1½ (fig. *4*). Figures *1*, *2* represent the entire specimen; *3*, the preserved part of the outer volution; and *4*, the inner volutions (that is, all but the portion of the specimen shown by figure *3*). (p. 676)

5—*Pseudoparalegoceras williamsi* Miller and Downs, n. sp. The holotype, ×1. (p. 677)

1

4

5

2

3

Miller and Downs, Pennsylvanian Cephalopoda

1

2

3

4

5

Miller and Downs, Pennsylvanian Cephalopoda

of essentially the same age. Also Thomas (1928, p. 293, pls. 10–12) and Delépine (1941, p. 97, pl. 8) have illustrated and described very closely related if not identical forms from such remote areas as northwestern Peru and northwestern Algeria. Almost certainly, the beds from which these specimens came are not greatly different in age from those at Winslow.

Altogether, the Winslow collections contain about two dozen nautiloids that we are identifying as *Mooreoceras* sp.; one that is made the holotype of *Knightoceras oxylobatum*, n. sp.; some 75 ammonoids that are designated *Pseudoparalegoceras williamsi*, n. sp.; and two for which the name *Winslowoceras henbesti*, n. gen. and sp., is being established. Of these, the nautiloids and the ammonoids which represent a new genus are not very helpful for precise stratigraphic correlations. Therefore, we are of necessity relying largely on *Pseudoparalegoceras williamsi*. As a general rule, it is not safe to attribute too much significance to a single species, rather than an assemblage; but in this case we are able to make direct comparisons of numerous large well preserved individuals from both the Winslow and the Atoka localities, and they show about the same size range and are even lithologically almost identical, being preserved as internal molds composed of ferruginous sandstone.

The discovery and occurrence of this fauna are described by the following statement which Mr. Henbest kindly prepared at our request.

STRATIGRAPHIC AND GEOGRAPHIC LOCATION[1]

LLOYD G. HENBEST

Location.—All the specimens described in this report were collected from a single locality in the town of Winslow, approximately 800 feet south of the Winslow railway station, and near the center of the south ½, sec. 13, T. 13 N., R. 30 W., Winslow quadrangle, Washington County, Arkansas. The source is a calcareous, ferruginous sandstone less than one foot thick, that is exposed in a creek bed where this stream empties into the east gutter of the cut on the Saint Louis-San Francisco Railroad 430 feet north along the tracks from the north end of the railroad tunnel.

This fossil locality was discovered in 1936 and a large collection was made. Later Dr. G. H. Girty and I collected additional specimens. In 1944 and in 1947, I revisited the locality and obtained further substantial collections.

Stratigraphic position and significance.—The bed from which these fossils were obtained is designated in the following description of the section as stratigraphic unit 7 (see text figure 1) and should not be confused with stratigraphic unit 2, in which cephalopods that are to be the subject of a later paper were recently found.

Stratigraphic unit 7 and associated beds lie in the lower part of the "Winslow formation" of Adams (1904, p. 29) redefined by Purdue (1907, p. 3) as already noted by Miller and Downs. A reconnaissance along the railroad and highway northeastward to the nearest exposure of the contact of the "Winslow formation" and the Morrow group indicated that the cephalopod bed lies 125 to 150 feet above the base of the "Winslow formation." In the hill five-eighths of a mile southwest of Brentwood Station, peculiar sandstone beds like those associated with the cephalopod-bearing bed at Winslow were observed at a similar interval above the base of the formation.

The source bed lies in a rock series that contains several repetitious sequences of sediments. These repetitions seem to be

[1] Published by permission of the Director, United States Geological Survey.

EXPLANATION OF PLATE 102

FIGS. *1–5*—*Pseudoparalegoceras williamsi* Miller and Downs, n. sp. Three paratypes from a thin brown ferruginous sandstone bed about 125–150 feet above the base of the "Winslow formation" at its type locality on the eastern side of a ditch about 430 feet north of the north portal of the Saint Louis-San Francisco Railroad tunnel at Winslow, Washington County, Arkansas, ×1. Figures *1*, *2* represent one specimen, as do *4*, *5*. All are deposited in the U. S. National Museum. (p. 677)

characteristic of the lower part of the "Winslow" in Washington County. One of their striking features is a sandstone, or a thin

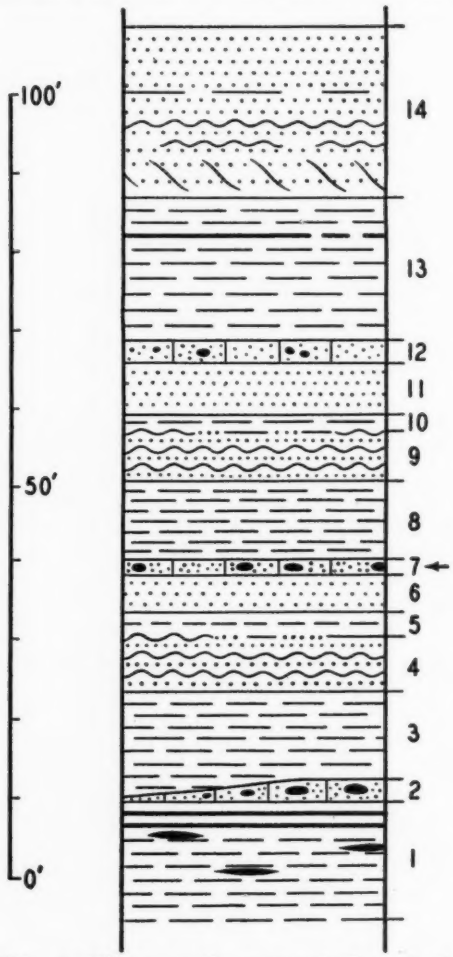


FIG. 1—Diagrammatic representation of the stratigraphic section exposed in the railroad cut at Winslow, Arkansas.

group of flaggy beds, that contains a great abundance of *Taonurus*? *colletti* Lesquereux, 1870, and a peculiar fossil that consists variously of a straight or bent or hook-shaped, conically septate tube, 5 to 15 mm., in diameter which in many cases appears as a string of nesting cones. *Taonurus*? *colletti* seems to be the fossil thallus of an extinct seaweed. The top of the *Taonurus*? bed interfingers with, or perhaps more commonly is capped by, a separate thin bed of sandstone that contains very sparsely scattered shells of brachiopods and mollusks. At Winslow, however, stratigraphic unit 7 bears in addition to the cephalopods a variety of brachiopods, pelecypods, and gastropods and contrastingly few bryozoans and Foraminifera.

Some features of the environment in which these cephalopod shells were deposited are revealed by the presence of more or less carbonaceous matter in the siltstone shale beds that alternate with the marine sandstone and *Taonurus*? sandstone units. Stratigraphic units 7 and 2 are dark, sideritic, apparently somewhat carbonaceous sandstone beds. These and the overlying shales evidently contained disseminated pyrite before weathering. Cross bedding, ripple marking, and thin bedding are commonly present in the sandstone units but are least conspicuous in the *Taonurus*? bed. These features suggest shallow water and generally poor circulation with the open sea, resulting in rather low-oxygen, high-hydrogen-sulfide water. The origin of *Taonurus*? is the subject of debate; accordingly, its ecologic significance is uncertain.

The limestones in the calcareous zones of the lower part of the "Winslow formation" comprise a very small part of the sediments and are generally leached or structurally altered almost beyond recognition at natural exposures. This is the result of the action of sulfurous acid produced by the weathering of disseminated sulfides and is the cause of the erroneous impression that the "Winslow" is nearly barren of marine invertebrate fossils. For this reason, these cephalopods and associated fossils are significant beyond their constituting new additions to the Pennsylvanian fauna. They help to bridge a gap that the lower part of the "Winslow" has represented for many years in the classification of the Pennsylvanian.

The occurrence of these cephalopods is unusually significant. The locality is in a region of little structural complication and it is sufficiently near the type areas of the Morrow group, and each of its subdivisions, that we can determine accurately its stratigraphic relations with the Morrow fauna, the best-known fauna of lower Pennsylvanian age, and with the other beds of the lower part of the "Winslow formation,"

which represent sediments of very early middle Pennsylvanian age. The succession of Pennsylvanian formations from the base of the Morrow group in Washington County westward and northwestward to the base of the Permian in northern Oklahoma and central Kansas is perhaps unique in the combination of (1) its completeness paleontologically and stratigraphically, (2) its relatively undisturbed structure, and (3) its almost unbroken succession of exposures of the formations in imbricating contacts. For these reasons it is becoming a standard for the Pennsylvanian generally. These "Winslow" cephalopods occupy a key position in that succession.

The stratigraphic section exposed in the cut of the Saint Louis-San Francisco Railroad between the north end of the tunnel and the railway station at Winslow is as follows:

Stratigraphic Unit	*Thickness Ft.*	*In.*	*Description*
14	22		Sandstone, massive at base and top, thin to irregularly bedded in middle, brown, friable, more or less ferruginous and earthy; some evidence of local cross bedding at base; *Taonurus? colletti* identified with some uncertainty in upper part.
13	19		Shale, very dark-gray, finely laminated, soapy feel; weathers to rather intense brownish medium-gray; sideritic stringer 3 feet below top bears poorly preserved cephalopods.
12	1	6	Sandstone, spongy, limonitized, originally contained much lime and numerous marine invertebrate fossils; original character and fossils mostly destroyed by replacement of lime by limonite.
11	5–6		Sandstone, closely resembles unit 6 below; crowded with carbonaceous remains of a hook-shaped conically septate organism.
10	1	6	Shale, very dark-gray, finely laminated, soapy feel, weathers brown.
9	6		Sandstone, fine-grained, thin-bedded to shaly in natural exposures, ripple-marked with clay or silt partings, brownish medium-gray; intergrades with unit 10 above.
8	10		Shale, very dark-gray, weathers to brownish medium-gray, finely laminated, soapy feel.
x	x	x	Fault. Stratigraphic displacement apparently only a few feet. Unit 11 may be a repetition of unit 6, although they seem to be different beds.
7	1	10	Conglomerate, intense reddish-brown, limonitic, spongy, soft when wet, originally composed of sand, lime, and locally, numerous claystone cobbles; external and internal molds of cephalopods, pelecypods, and gastropods common to very abundant; a limited fauna of brachiopods and bryozoans also present; **the source of the cephalopods described by Miller and Downs.**
6	3 to 4	10 0	Sandstone, a single massive bed, fine- to medium-grained, light-gray, *Taonurus? colletti* and very abundant hook-shaped, conically septate fossils which may be part of *Taonurus?;* large specimen of coiled cephalopod found about 1 foot below top of bed.
5	2	6	Shale, very dark-gray, finely laminated.
4	6 to 7	6 0	Sandstone, fine to very fine grained, hard, light-gray to white, ripple-marked, with numerous clay partings, probably weathers to thin-bedded flagstone.
3	12		Shale, very dark-gray, finely laminated, soapy feel.
2	0 to 1	4 8	Sandstone, ferruginous, calcareous, conglomeratic with claystone cobbles; contains numerous cephalopods at a locality 80 feet north of the tunnel; perhaps a lens in the shale rather than a continuous bed.
x	x	x	Fault, small, displacement compensated in measurements.
1	12	6	Shale, very dark-gray, finely laminated, soapy feel, middle to upper parts contain isolated to continuous stringers of sideritic concretions; calcareous at top; base not exposed.
0	0	0	Track level at portal at north end of railroad tunnel. (Measurements by hand level and tape.)

SYSTEMATIC PALEONTOLOGY

MOOREOCERAS sp.

The collections under consideration contain about two dozen small fragmentary internal molds of orthoconic nautiloids. The largest of these is about 15 mm. in diameter, and the length of the longest one (a small

specimen) is about 40 mm. In all of them the conch is moderately expanded orad and circular or nearly so in cross section. The septa are saucer-shaped and fairly close together, and the sutures are straight and directly transverse. The siphuncle is small, at least at its passage through the septa, and, with the possible exception of one crushed specimen, it is located about midway between the center and the venter.

Remarks.—The preservation of these specimens leaves much to be desired, and none of them seem to merit illustration. We were not able to determine the nature of the surface markings of the test or the structure of the siphuncle. However, all of the characters that can be ascertained seem to coincide well with those of typical *Mooreoceras*, and almost certainly these specimens are referable to that genus. However, the one crushed individual that appears to have a central siphuncle may possibly belong in *Pseudorthoceras*, *Michelinoceras*, or some similar genus.

Occurrence.—Thin brown ferruginous sandstone bed about 125–150 feet above the base of the "Winslow formation" at its type locality along the eastern side of a ditch about 425–475 feet north of the north portal of the Saint Louis-San Francisco Railroad tunnel at Winslow, Washington County, Arkansas.

Repository.—U. S. National Museum

KNIGHTOCERAS OXYLOBATUM Miller and Downs, n. sp.
Plate 101, figures 1–4

This species is based on a single rather well preserved internal mold that represents much of three volutions of a phragmacone that attained a diameter of at least 70 mm. The conch is regularly expanded orad, is depressed dorsoventrally, and is sublenticular in cross section but (except in most of the first volution) slightly impressed dorsally. The internal mold is very narrowly rounded or subangular laterally and broadly rounded ventrally and dorsally (except for the impressed zone). However, in the extreme adoral portion a very slight median concave zone is developed along the venter. In general, the ventral and dorsal sides of the conch are about equally arched. At the adoral end the conch is about 47 mm. wide and 27 mm. high, and the dorsal impressed zone is about 24 mm. wide and 3½ mm. deep. In the inner volutions, the dorsal impressed zone is less prominent. It starts to form slightly apicad of the adoral end of the first volution of the conch.

The umbilicus is large, open, and almost certainly perforate. Its diameter is equal to about three-fifths that of the specimen.

No trace of the surface markings of the test is discernible on the only known representative of this species. However, on the ventral side of the preserved part of the internal mold of the intermediate volution, there is a suggestion of a median longitudinal raised line and others parallel to it.

The camerae are moderately short, and the concavity of the septa is about average. The sutures form very slight broadly rounded lobes along the venter and on the umbilical walls, and as they cross the dorsal impressed zone they form relatively deep somewhat acuminate lobes the tips of which are rounded.

The siphuncle is small, at least at its passage through the septa. It is central in

---

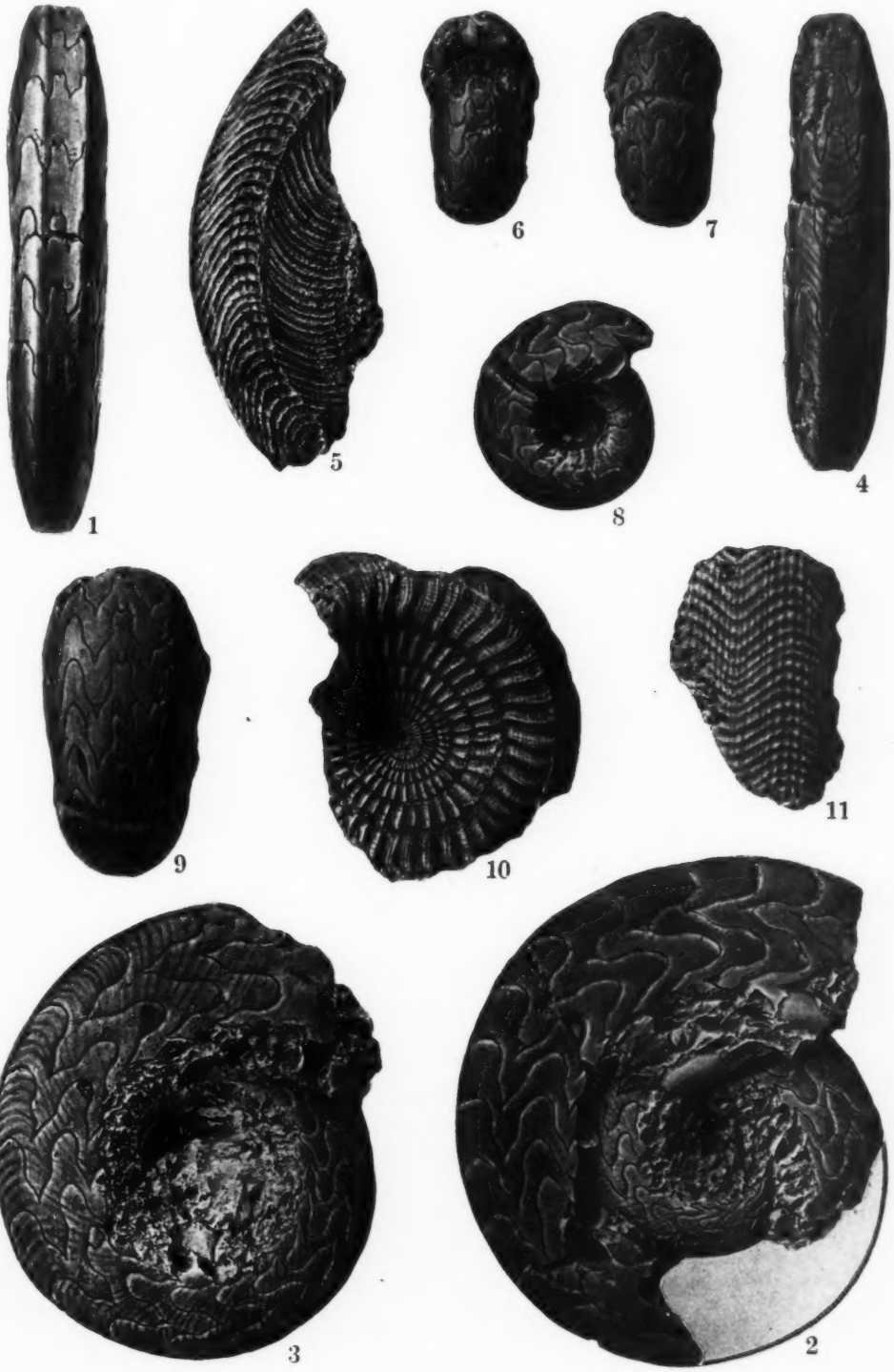
EXPLANATION OF PLATE 103

All illustrated specimens are deposited in the U. S. National Museum. With the exception of figures *10, 11*, they are from a thin brown ferruginous sandstone bed about 125–150 feet above the base of the "Winslow formation" at its type locality on the eastern side of a ditch about 430 feet north of the north portal of the Saint Louis-San Francisco Railroad tunnel at Winslow, Washington County, Arkansas. Figures *10, 11* represent specimens from the Hale formation on the eastern side of Gaither Mountain near Harrison, Boone County, Arkansas.

FIGS. *1–5*—*Winslowoceras henbesti*, n. gen. and sp. The holotype. Figures *1, 2* represent the entire specimen, ×1; *3, 4* illustrate all of the specimen but the adoral three-fifths of the outer volution, ×1½; *5* portrays an artificial cast of the adoral portion of the penultimate volution, ×2. (p. 679)

6–9—*Pseudoparalegoceras williamsi*, n. sp. Two of the paratypes, ×1½ (figs. *6–8*) and ×1 (fig. *9*). Figures *6–8* represent one specimen. (p. 677)

10, 11—*Gastrioceras branneri branneri* Smith. Two artificial casts, ×1½. (p. 680)



Miller and Downs, Pennsylvanian Cephalopoda

position, or nearly so, but near the adoral end of the first volution it is distinctly nearer the venter than the dorsum.

Remarks.—The angularity of the internal lobes of the sutures of this species differentiates it from all other representatives of the genus with which we are familiar. It is only moderately close to the genotype, *K. missouriense* Miller and Owen of the Cherokee of west-central Missouri, which is known from only a single small living chamber. *K. abundum* Miller, Lane, and Unklesbay of the Winterset limestone of west-central Missouri, *K. tiltnoi* (Miller, Dunbar, and Condra) of the Bethany Falls limestone of south-central Iowa, and *K. subcariniferum* (Tzwetaev) of the Dewiatowo oölite (early Pennsylvanian) of central European Russia are all relatively large forms that are at least superficially similar.

Occurrence.—Thin brown ferruginous sandstone bed about 125–150 feet above the base of the "Winslow formation" at its type locality along the eastern side of a ditch about 425–475 feet north of the north portal of the Saint Louis-San Francisco Railroad tunnel at Winslow, Washington County, Arkansas.

Holotype.—U. S. National Museum.

PSEUDOPARALEGOCERAS WILLIAMSI
Miller and Downs, n. sp.
Plate 101, figure 5; Plate 102, figures 1–5; Plate 103, figures 6–9

(?)*Phaneroceras compressum* [part] PLUMMER and SCOTT, 1937, Texas Univ. Bull. 3701, pp. 15, 16, 30, 33, 191–193, 194, 220, 281, pl. 9, figs. 4–10; pl. 11, fig. 13.

All but two of the ammonoids in the Winslow collections under consideration belong in this species, which is based on about 75 specimens. The best of these, represented by figure 5 on plate 101, is designated the holotype. It is an internal mold of much of a phragmacone that was at least 80 mm. in diameter. Near the adoral end of the preserved part of this specimen, the conch is about 33 mm. high and its corresponding width was about 40 mm. The cross section is helmet-shaped as the conch is compressed laterally, rounded ventrally and ventrolaterally, flattened laterally, subangular dorsolaterally, and deeply impressed dorsally. The umbilicus is moderately large and open. The umbilical shoulders are subangular, and the umbilical walls are flat and steep, being almost normal to the lateral zones of the conch. The diameter of the umbilicus is equal to about three-eighths that of the specimen, and the maximum diameter attained by the umbilicus of the preserved part of the holotype measures almost 30 mm. The paratype represented by figures 4 and 5 on plate 102 shows that in this species the phragmacone attained a diameter of at least 90 mm. and that the corresponding diameter of the umbilicus was about 31 mm.

None of the specimens retains traces of the surface markings. However, the holotype and the paratypes represented by figures 1–3 on plate 102 and 6–9 on plate 103 show that the internal mold of the early mature portion of the conch bears prominent rounded transverse constrictions, of which there are three or four to the volution. These constrictions are slightly sinuous and they form broad shallow rounded lateral and ventral sinuses and narrowly rounded ventrolateral salients. No trace of them is present on the fully mature portions of the conch.

As shown by text figure 2, each mature suture forms a large prominently bifid ventral lobe with hastate prongs, and on either side of it a narrowly rounded more or less V-shaped first lateral saddle with sinuous flanks, a large hastate first lateral lobe, an asymmetrical rather narrowly rounded second lateral saddle, a shallower pointed lobe centering on the umbilical wall, a broad asymmetrical broadly rounded saddle that crosses the umbilical seam, a pointed spatulate internal first lateral lobe, and a narrow U-shaped internal first lateral saddle which extends to the deep narrow pointed spatulate dorsal lobe. All of the lobes are distinctly acuminate.

Remarks.—This species, which is named in honor of Dr. James Steele Williams, resembles *Pseudoparalegoceras compressum* (Hyatt) of the Bend group of central Texas, the holotype of which has a relatively large umbilicus. Plummer and Scott seem to have referred to that species a considerable variety of specimens, and as we have indicated in the synonymy some of these may well be referable to our species.

Plummer and Scott designated *P. compressum* as the type species of their genus *Phaneroceras*. However, as Miller and Furnish (1940, p. 529) have pointed out, that generic name should be suppressed as a synonym of *Pseudoparalegoceras*, which has priority. Also, in our opinion, the type species of *Eoparalegoceras* Delépine probably does not differ sufficiently from that of *Pseudoparalegoceras* to be regarded as generically distinct.

P. brasoense Plummer and Scott of the Strawn group of Texas, the Boggy formation and probably the Buckhorn asphalt of Oklahoma, and the Magdalena formation of New Mexico can be differentiated from our species by the fact that the umbilical lobe of its sutures centers outside the umbilical shoulder rather than on the umbilical wall.

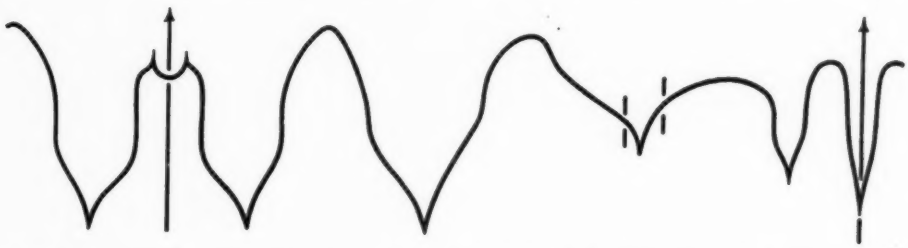


FIG. 2—Diagrammatic representation of a mature suture of *Pseudoparalegoceras williamsi*, n. sp., based on the adoral sutures of the specimen represented by figures 4 and 5 on plate 102, ×1½.

In another very similar form, *P. clariondi* (Delépine) of the early Upper Carboniferous of northwestern Africa, the umbilical lobe centers on or just inside the umbilical shoulder. *P. amotapense* (Thomas) of the early Pennsylvanian of northwestern Peru has sutures (and other features) that are very much like those of *P. williamsi*, and it may be that these two forms can not be differentiated specifically; however, the sinuous transverse constrictions appear to be retained during later ontogenetic stages in South American specimens.

Occurrence.—Thin brown ferruginous sandstone bed about 125-150 feet above the base of the "Winslow formation" at its type locality along the eastern side of a ditch about 425-475 feet north of the north portal of the Saint Louis-San Francisco Railroad tunnel at Winslow, Washington County, Arkansas. Also the collections of Lewis M. Cline and those of John Britts Owen at the State University of Iowa contain a good many specimens from the Atoka sandstone north of Clarita, Cole County, Oklahoma, that appear to belong in this species—they are even lithologically similar.

Types.—U. S. National Museum.

Genus WINSLOWOCERAS Miller and Downs, n. gen.
Genotype: *Winslowoceras henbesti*, Miller and Downs n. sp.

Two conspecific specimens in the Winslow collections appear to represent a new genus, for which we propose the name *Winslowoceras*.

Conch moderately large and discoidal as whorls are compressed and greatly flattened laterally and ventrally and subangular ventrolaterally—at full maturity the lateral zones are almost parallel and the ventral zone is distinctly concave. Umbilicus moderately large and open. Surface of test bears prominent sinuous transverse lirae which form ventral sinuses and lateral salients and sinuses and which are crossed by a few longitudinal lirae. Each mature suture consists of ten lobes and an equal number of saddles; the ventral lobe is rather short and bifid whereas all of the other lobes are pointed and the saddles rounded.

The most distinctive features of this genus are the discoidal shape of the conch, the prominent surface markings of the test, and the shape of the sutures (particularly the relatively short ventral lobe). These serve to differentiate it readily from such genera as *Gastrioceras*, *Pseudoparalegoceras* and *Diabloceras*, with which it should be associated.

Bendoceras moorei Plummer and Scott of

the early Pennsylvanian of central and west Texas seems to resemble the genotype of *Winslowoceras* rather closely and is most probably congeneric—it can be distinguished specifically by means of the peculiar first lateral saddles of its sutures. Also, this genus probably includes the specimen from the Bend group of central Texas that was illustrated and described by Hyatt (1893, p. 474, text figs. 52–55) who erroneously referred it to *Paralegoceras iowaense* (Meek and Worthen)—see Plummer and Scott (1937, p. 212) for a discussion of this form.

WINSLOWOCERAS HENBESTI
Miller and Downs, n. sp.
Plate 103, figures 1-5

Both of the specimens of this species are of essentially the same size and shape, but one of them, designated the holotype (pl. 103, figs. 1-5), is much better preserved. It, like the paratype, is completely septate and therefore represents only phragmacone. The maximum diameter of this individual, measured from the adoral end of the venter across the umbilicus to the opposite side of the specimen, is about 73 mm., and the part of the conch that is represented attains a maximum width of about 14 mm. and a maximum height of about 24 mm. The cross section of the whorls is subrectangular as the conch is greatly flattened ventrally and laterally, subangular ventrolaterally, and only slightly impressed dorsally. At full maturity the ventral zone is slightly but distinctly concave and the lateral zones are almost parallel, though the maximum width of the conch is attained in the general vicinity of the umbilical shoulders. Peculiarly, the umbilical portions of the conch are not preserved on any visible portion of either of the specimens, but it can be determined that the umbilicus of both of them attained a diameter of about 33 mm.

The surface of the test bears prominent sinuous transverse lirae, and a few longitudinal ones on the ventral portion of the lateral zones (pl. 103, fig. 5). Each of the transverse lirae forms a deep subangular ventral sinus and on either side of it a high asymmetrical rounded salient (located on the ventral portion of the lateral zones) followed by a relatively shallow broadly rounded lateral sinus. Traces of these transverse markings are clearly discernible on the internal mold of the penultimate volution of the holotype (pl. 103, figs. 4,5).

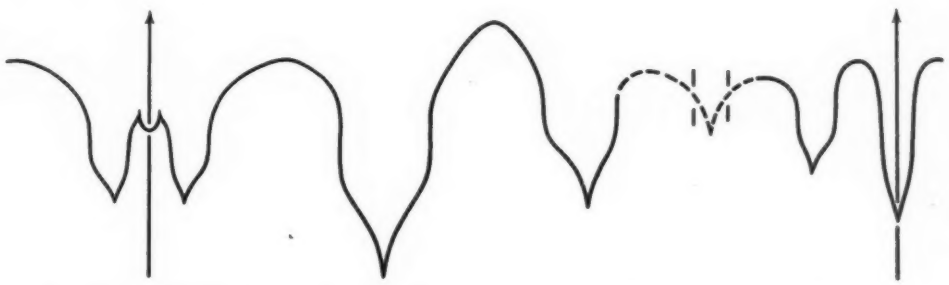


FIG. 3—Diagrammatic representation of a mature suture of *Winslowoceras henbesti*, n. sp., based on the adoral sutures of the holotype, ×3.

As shown by text figure 3, each mature suture forms a short broad prominently bifid ventral lobe the prongs of which are narrow and asymmetrical, and on either side of it a high U-shaped first lateral saddle, a deep hastate acuminate first lateral lobe, a high narrowly rounded second lateral saddle, a second lateral lobe that is similar to the first but smaller, a third lateral saddle (of which the exact shape is not known) in the region of the umbilical shoulder, an umbilical lobe (the size and position of which can not be determined from either of the specimens), a saddle (also of unknown shape) that appears to center near the umbilical seam, an asymmetrically V-shaped internal second lateral lobe, and a narrow U-shaped internal first lateral saddle that extends to the deep pointed spatulate dorsal lobe.

Remarks.—This species, which is named in honor of Mr. Lloyd G. Henbest, is quite distinct from all of the others with which we are familiar. *W.? moorei* (Plummer and Scott) of the early Pennsylvanian of central and west Texas is somewhat similar, but the adoral portions of the first lateral saddles of its sutures are very asymmetrical. The specimen from the Bend group of central Texas that Hyatt (1893, p. 474, text figs. 52–55) erroneously referred to *Paralegoceras iowaense* (Meek and Worthen) is also superficially similar to those we describe but its conch is not as strongly compressed and its sutures seem to be considerably different in detail.

Occurrence.—Thin brown ferruginous sandstone bed about 125-150 feet above the base of the "Winslow formation" at its type locality along the eastern side of a ditch about 425–475 feet north of the north portal of the Saint Louis-San Francisco Railroad tunnel at Winslow, Washington County, Arkansas.

Types.—U. S. National Museum.

APPENDIX

On October 6, 1938, Messrs. Lloyd G. Henbest, O. J. Henbest, Tom Millard, and Hugh D. Miser collected about one hundred limestone slabs from the Lower Pennsylvanian Hale formation on the east side of Gaither Mountain, Harrison quadrangle, northwestern Arkansas. These were recently loaned to us for study through the courtesy of Messrs. Lloyd G. Henbest and James Steele Williams of the U. S. Geological Survey. They contain some brachiopods, pelecypods, and particularly gastropods, but few identifiable cephalopods. However, from two external molds, we were able to prepare casts that are quite satisfactory for study (pl. 103, figs. 10,11). Both of these are referable to *Gastrioceras branneri branneri* Smith, and they are strikingly similar lithologically and morphologically to comparable portions of a moderately large representative of that variety which was illustrated by Miller and Moore (1938, pl. 44, figs. 11,12). That individual came from the same zone and locality and it is available for direct comparisons. Specimens that belong to the same variety are known to occur in the Hale formation at other localities in northwestern Arkansas, in the Morrow group of northeastern Oklahoma, in the Union Valley formation of south-central Oklahoma, and probably in the Bend group of central Texas.

As noted by Miller and Owen (1944, pp. 422–423), Plummer and Scott's genus *Branneroceras*, of which the type by original designation is *Gastrioceras branneri*, is to be suppressed as a synonym of *Gastrioceras* Hyatt, which has priority. Miller and Owen also presented a complete up-to-date synonymy of *G. branneri branneri*.

REFERENCES

Adams, G. I., Purdue, A. H., and Burchard E. F., 1904, Zinc and lead deposits of northern Arkansas (with a section on the determination and correlation of formations by E. O. Ulrich): U. S. Geol. Surv., Prof. Paper 24, pp. 1–118, pls. 1–27.

Delépine, Gaston, 1941, Les goniatites du Carbonifère du Maroc et des confins Algéro-Marocains du sud (Dinantien-Westphalien): Protect. l'État Français Maroc, Dir. Gén. Trav. Pub., Div. Mines Géol., Serv. Géol., Notes et Mém. 56, pp. 1–110, pls. 1–8.

Hyatt, Alpheus, 1893, Carboniferous cephalopods, Second paper: Texas Geol. Surv. 4th Ann. Rept., pp. 377–474.

Miller, A. K., and Furnish, W. M., 1940, Studies of Carboniferous ammonoids, Parts 5–7: Jour. Paleontology, vol. 14, pp. 521–543, pls. 62–65.

——, and Moore, Carl A., 1938, Cephalopods from the Carboniferous Morrow group of northern Arkansas and Oklahoma: Jour. Paleontology, vol. 12, pp. 341–354, pls. 43, 44.

——, and Owen, John Britts, 1944, The cephalopod fauna of the Pennsylvanian Union Valley formation of Oklahoma: Jour. Paleontology, vol. 18, pp. 417–428, pls. 63–68.

Plummer, F. B., and Scott, Gayle, 1937, Upper Paleozoic ammonites in Texas; The geology of Texas, Volume III, part 1: Texas Univ. Bull. 3701, pp. 1–516, pls. 1–41.

Purdue, A. H., 1907, Description of the Winslow quadrangle: U. S. Geol. Survey, Geol. Atlas of the United States, Winslow folio, Arkansas-Indian Territory, No. 154, pp. 1–6, 2 maps, 1 columnar section.

Thomas, H. Dighton, 1928, An Upper Carboniferous fauna, from the Amotape Mountains, north-western Peru: Geol. Mag., vol. 65, pp. 146–152, 215–234, 289–301, pls. 5–8, 10–12.

Wilmarth, M. Grace, 1938, Lexicon of geologic names of the United States (including Alaska) . . . : U. S. Geol. Survey Bull. 896, pp. 1–2396 (in two volumes).

JOURNAL OF PALEONTOLOGY, VOL. 22, NO. 6, PP. 681–724, PLS. 104–115, 18 TEXT FIGS., NOVEMBER 1948

PTERIDOSPERM MALE FRUCTIFICATIONS: AMERICAN SPECIES OF *DOLEROTHECA*, WITH NOTES REGARDING CERTAIN ALLIED FORMS

JAMES M. SCHOPF
U. S. Geological Survey, Washington, D. C.

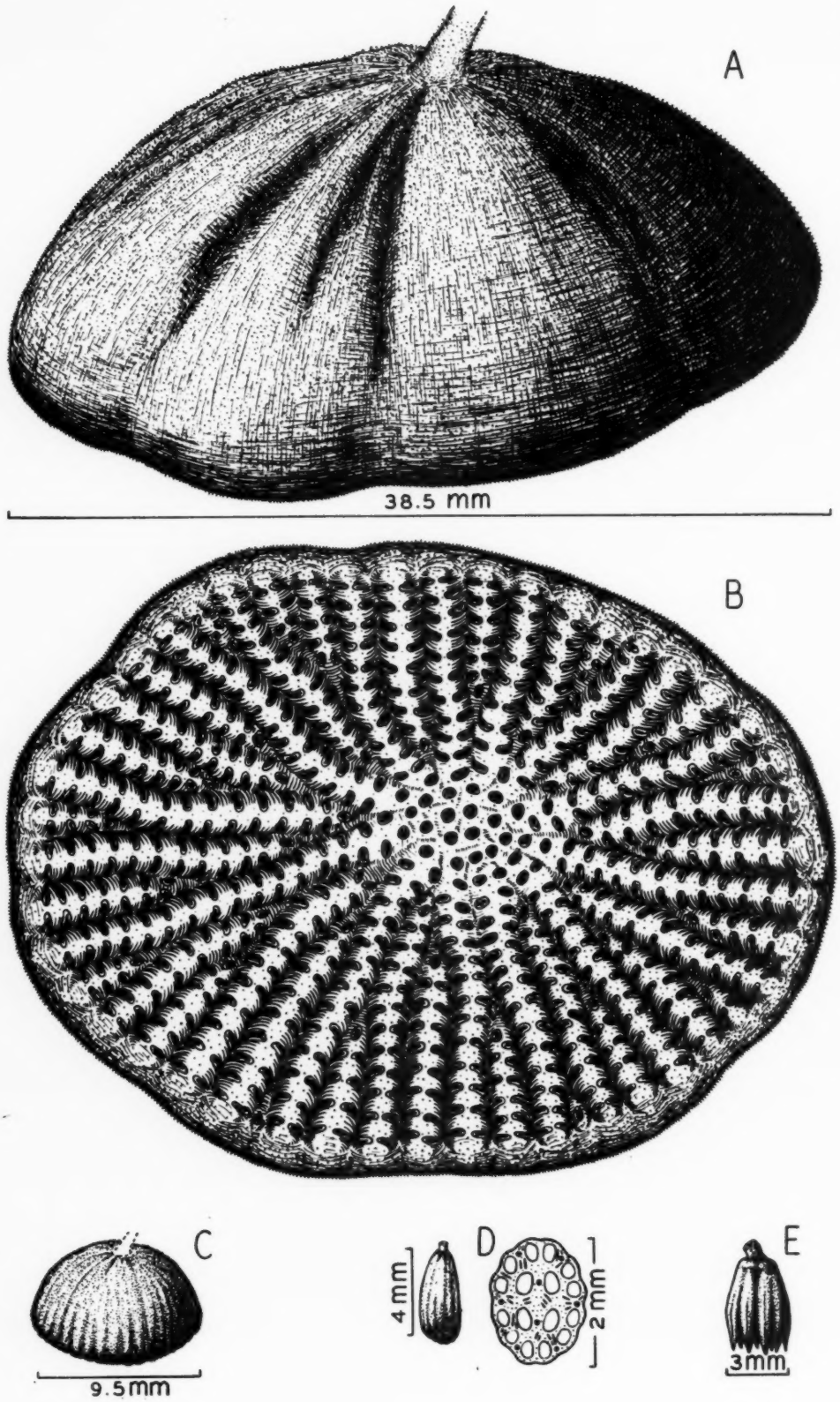
ABSTRACT—*Dolerotheca* includes a group of pteridosperms (Medullosaceae) characterized by very large and unusual pollen-bearing organs. Their botanical pertinence to plant microfossil studies and to phyletic theories, as well as their rarity in good preservation, lends considerable interest to these fossils. The morphology of the polleniferous organs, or male fructifications, is reviewed preliminary to taxonomic treatment of the new American material. Three new species are described in considerable detail both as to general external form and internal organization—a result possible only because of preservation in the limestone concretions in coal beds known as coal balls. The species of *Dolerotheca* are assembled in a new sub-tribe called the Dolerothecinae. The evidence for relating these forms with other coal-ball fossils known as *Myeloxylon*, and, in turn, with *Medullosa*, is discussed with particular reference to one species where the peduncular organ of attachment seems to be preserved. Notes are also included regarding a specimen of *Dolerotheca* preserved in surface imprint in an ironstone concretion, and regarding the allied Whittleseyinean group classed as *Codonotheca*. The relationships and comparative anatomy of *Dolerotheca* with other pteridosperm groups that present homologous features are discussed and a tentative evolutionary interpretation presented. *Heterotheca* of the Lower Carboniferous appears to represent a plausible ancestral type, combining features of both the lyginopterid and medullosan lines of descent. The morphology of *Dolerotheca* suggests, however, that evolutionary modification has been by elaboration and septation of a single telomic structure rather than by adnation and concrescence of many.

INTRODUCTION

THE male fructifications of pteridosperms are less well understood than most of the other organs pertaining to this large group of ancient plants. The fact that a considerable number of the Paleozoic fern-like plants bore seeds and hence were not true ferns, in spite of their highly dissected or pinnatifid leaves, became established about 45 years ago. Since then a number of pteridosperm seed types have become well known; on the other hand an equivalent amount of information has not been obtained about the male fructifications despite the fact they must have been numerous. Some of the first recognized pteridosperms seemed to have male fructifications resembling the synangia of ferns. These organs were presumed to be conservative and little modified in the evolutionary transition from the free-sporing to the seed habit. However it has become clear during the last fifteen years that certain other groups of pteridosperms possessed male fructifications that differ radically from organs known in ferns. A more complete understanding of the characteristics and the nature of the diversity of male fructifications in pteridosperms will have important influence on ideas of phylogeny and relationship among this large, chiefly Paleozoic, plant alliance.

Among the pteridosperms the plants classified as *Dolerotheca* display conspicuous differences with regard to their male fructifications. Such fructifications of *Dolerotheca* have not been commonly reported, and up to the time specimens here described were discovered, only a single fragment was known which showed well preserved tissue structures. A few surface impressions and coalified compressions of similar fructifications have been recognized, but these are difficult to interpret and naturally afforded much less conclusive information about their structural organization than do the specimens described below.

These new fossils from coal balls have the cells preserved in almost perfect detail. Coal


A
38.5 mm
B
C
9.5mm
4 mm
D
1
2mm
E
3mm

balls are calcareous, siliceous, or dolomitic concretions that formed in some Carboniferous peat beds, in which mineral matter solidly infiltrated, enclosed, and preserved plant organs and other peaty materials with remarkable perfection. The enclosed plant materials were protected from subsequent alteration, whereas the adjacent unmineralized peat became much compressed and was transformed to coal. Consequently it is possible to describe the *Dolerotheca* fructifications found in coal balls in considerable detail and to compare their anatomical and tissue structure with that of more conventional organs of spore or pollen production.

This new information permits more adequate comparison with the fructifications of other pteridospermous plants than was previously possible and thus assists in interpretation of relationships and phylogeny. Because only a few of the fossils that can be compared with *Dolerotheca* are as amply described, and because the organization of *Dolerotheca* fructifications is relatively novel, the writer's present phylogenetic interpretation is tentative, a working hypothesis that later discoveries may or may not confirm. A full appreciation of the significance of *Dolerotheca* may be impossible for some considerable time.

These descriptions of fossil fructifications should also help to clarify the relationship of certain common types of plant microfossils that are abundant in coal. The value of isolated spore and pollen types in identifying and tracing individual coal beds is a matter of current investigation. Their effective use depends not only on knowledge of their stratigraphic distribution but also on a knowledge of the natural groups of plants which they represent. From such knowledge it may be possible to attribute certain varieties of coal material to certain kinds or to various associations of plants. Spores and pollens actually found in their parent fructifications indicate affinities of at least some of the similar spores and pollens isolated from coal and thus facilitate a more accurate biologic classification of the abundant microfossils. Isolated spores of the type borne by *Dolerotheca* are usually identified with the genus *Monoletes*, in part, unless their more precise affinity can be established (Schopf, Wilson, and Bentall, 1944). At present, when subsidiary information about the organs that bore them is lacking, the isolated spores cannot be assigned to a less generalized group.

Dolerotheca is believed to be allied with the Medullosaceae as broadly defined. The writer believes that the Medullosaceae includes the genera *Alethopteris*, *Callipteris*, *Myeloxylon*, *Medullosa*, *Rotodontiospermum*, *Trigonocarpus* (at least in part) and some other allied genera typified by their seeds. *Neuropteris*, and some other genera typified by characteristics shown by leaves and fronds, may possibly be allied with this family, in spite of the fact that their relationship to the type genus, *Medullosa*, has not been indicated by recent studies.[1]

The comparison of *Dolerotheca* with fructifications of the Whittleseyineae tends to confirm the alliance of this subtribe within the medullosan family.

Halle's brillant research (1933) on the structure of the Whittleseyinean types was based largely on coalified compression specimens. With some hesitation he included

[1] Schopf (1937), Steidtmann (1944) and Andrews (1945) all present evidence of alliance between *Medullosa* and *Alethopteris*.

EXPLANATION OF FRONTISPIECE

External Appearance of Male Fructifications of Pteridosperms
Figures (except Section Diagram D) are drawn to the same scale

A. *Dolerotheca formosa*, surface reconstruction showing proximal features.
B. *D. formosa*, surface reconstruction showing distal features.
C. *D. villosa*, surface reconstruction showing proximal features.
D. *Heterotheca grievii* (left), Surface reconstruction showing side view; (right) cross-section, diagrammatic, black heavy dots—vascular bundles, hatch lines—sclerotic tissue, round open areas—sporangia. Based on description, figures and measurements reported by Miss Benson (1922).
E. *Telangium scotti*, surface reconstruction, according to description, figures and measurements reported by Miss Benson (1904).

Dolerotheca as a member of the Whittleseyinean subtribe. The structure of *Dolerotheca* is now shown to be sufficiently different so that its separation as another subtribe seems advisable; the alliance of the new subtribe Dolerothecineae (here proposed; see p. 687) with the Whittleseyineae can scarcely be doubted and only the taxonomic decision as to how this relationship should most appropriately be expressed can involve any difference of opinion. In this regard the writer has followed Halle in utilizing the subtribal category because he believes the Dolerothecinean group merits recognition on a par with the Whittleseyinean group.

The Medullosaceae is an important family which includes several genera having extensive distribution in the Euro-American floral province of the Carboniferous and Permian, with some species of special stratigraphic value. It therefore seems remarkable that so little has been known in general about the male fructifications of these plants. Undoubtedly they were actually much more common than would appear from scattered references in the present literature. They may not have been recognized in some instances because they appear to have been deciduous shortly past maturity and they may have disintegrated readily after they dropped from their attachment on the plant. Furthermore, in their more common preservation as compressions, the male fructifications frequently do not show very distinctive megascopic features and the characteristics they do show have in the past been difficult to interpret. The data to be presented relative to their organization and microscopic characteristics may aid considerably in facilitating recognition of such organs in various states of fossil preservation. Additional records and observations are needed to establish their use in stratigraphic paleontology.

SUMMARY OF MORPHOLOGY AND ORGANIZATION OF DOLEROTHECA

Detailed information about the plants classified as *Dolerotheca* is lacking for all parts except the male fructification, and characteristics of such fertile parts provide the only basis for identification. Evidence of histology and association point to the very great likelihood that the fructifications were borne on fronds of the same type as *Myeloxylon* and *Alethopteris*. The manner in which the male organs were connected to the plant is not precisely known, and only in *Dolerotheca reedana* has a probable connective organ (described as a peduncle (?), c.f., p. 710) been observed. However, the peduncle (?) is not in actual attachment. The evidence at hand suggests that the organs were shed from their connection with the plant soon after maturity, and that their early abscission left a very inconspicuous scar, both on the parent axis and on the fructification itself.

The male fructifications of *Dolerotheca* are broadly bell-shaped and include numer-

---

EXPLANATION OF PLATE 104

FIG. *1*—*Dolerotheca formosa*, longitudinal section—fructification is enclosed in a dense mat of *Alethopteris* leaves. From coal ball 219 B1 (t 1).

2—Same as above, section from opposite side of saw kerf. From coal ball 291 Cl (b 1).

3—*D. formosa*, transverse section (peel) of fructification across the irregular distal (dehiscence) surface. From coal ball 129 A (t 7).

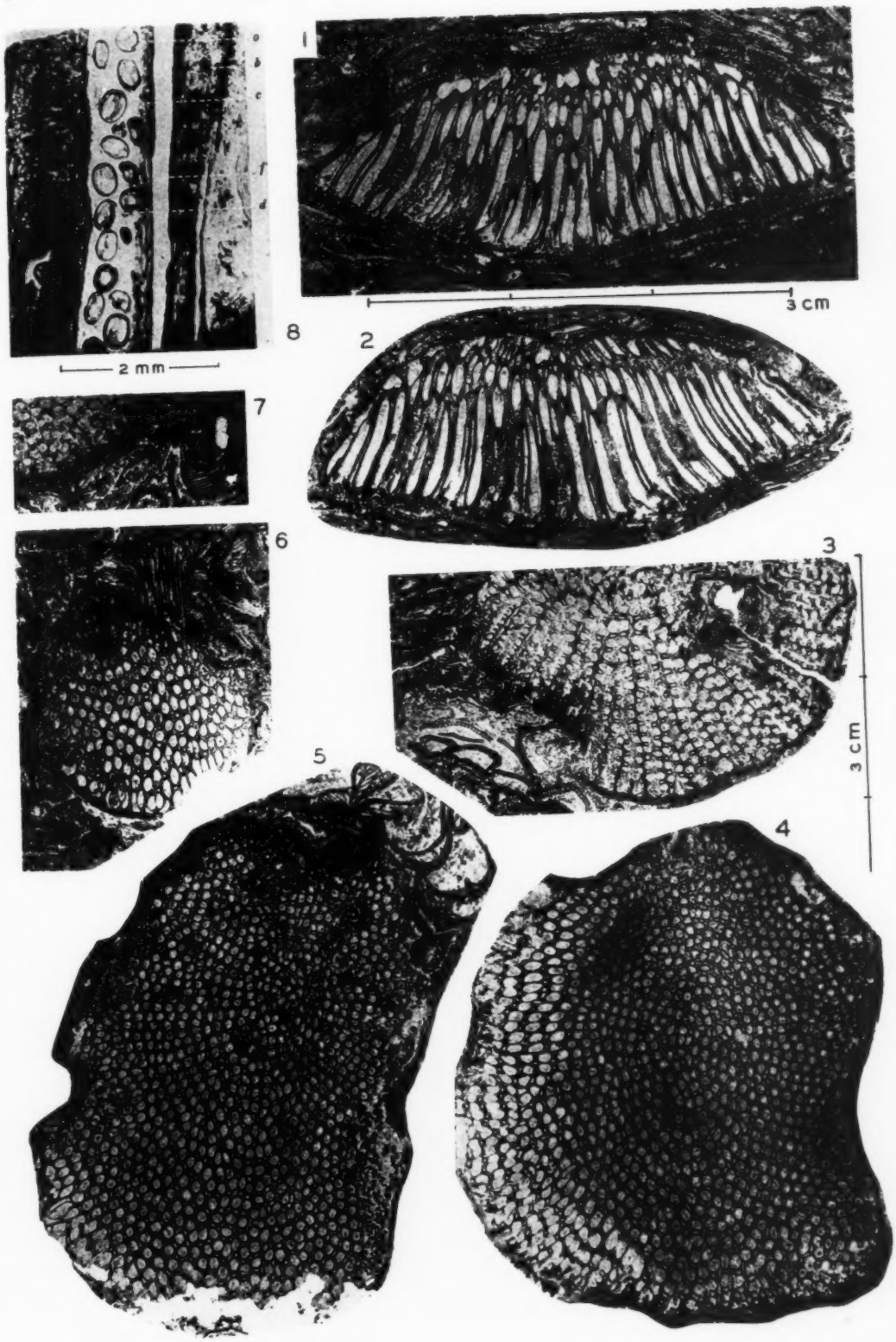
4—*D. formosa*, transverse section of fructification taken at a higher level than figure *3*, intersecting dehiscence tissue only on the left. From coal ball 129 A (t 22), scale same as figure *3*.

5—Same as above, section taken at a higher plane. From coal ball 129 A (t 25), scale same as for figures *3* and *4*.

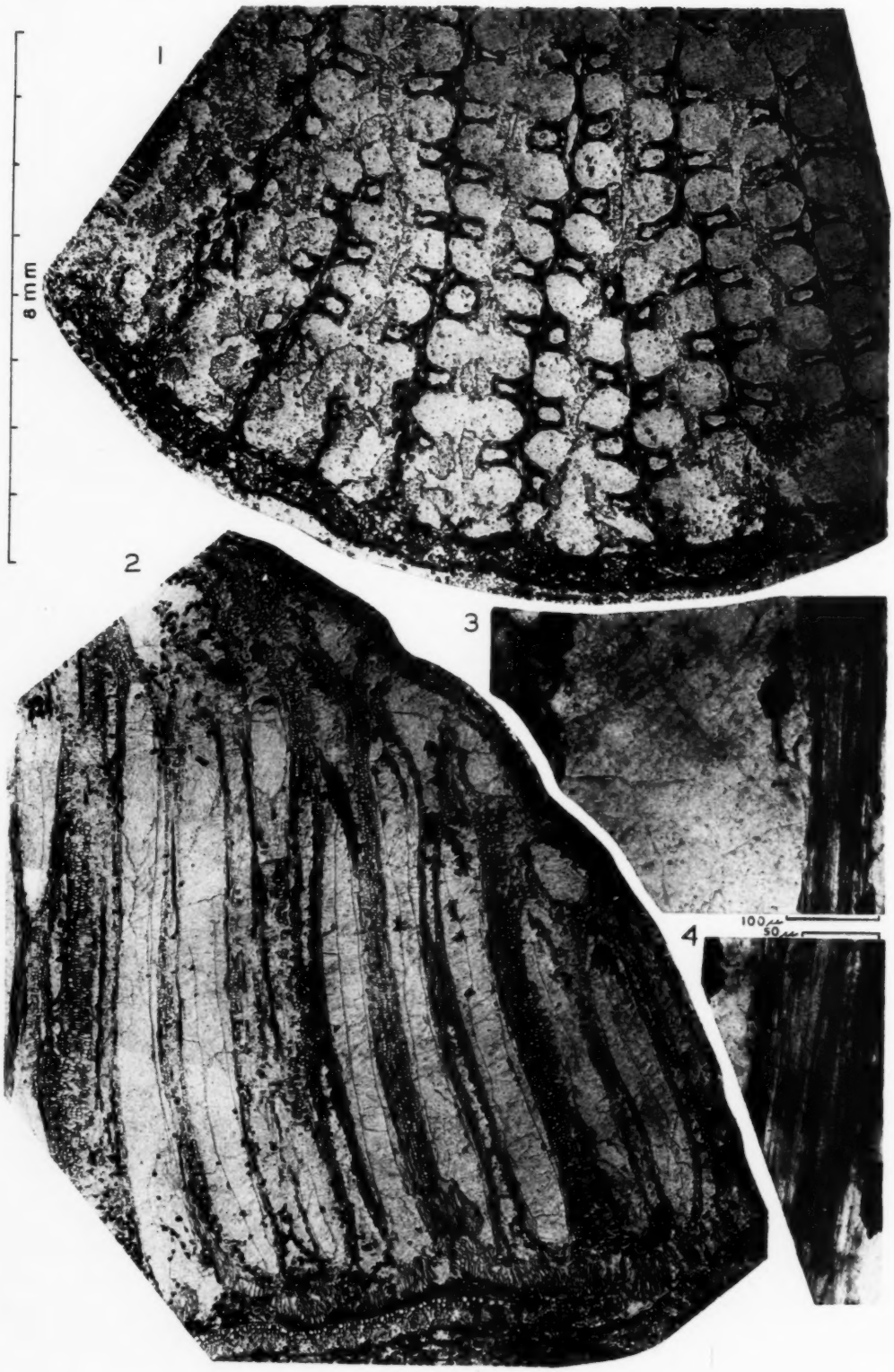
6—Same as above, section at the top of fructification. The fragment of "sparganum" cortex shown in the upper center does not seem to be attached. Note horizontal sections of *Alethopteris* leaves showing venation. From coal ball 129 A (t 38), magnification same as figures *3* and *4*.

7—*D. formosa*, transverse section of a different fructification at level of dehiscence tissue with associated *Alethopteris* leaves. From coal ball 129 A (t 38), same scale as figures *3* and *4*.

8—*Dolerotheca fertilis* (Renault) Halle, longitudinal section of sporangium and spores, o. d, spores; b, intersporangial tissue; c, sporangial membrane (?); f, lysigenous tube ?. Copeid for comparison from Renault (fig. 1, Pl. XIII, 1902).



Schopf, *Dolerotheca formosa* n. sp., *D. fertilis* Halle



Schopf, *Dolerotheca formosa* n.sp.

ous long tubular sporangia immersed completely in tissue. The structure is large and massive and quite unlike any of the conventional types of polleniferous structures (see, for example, the discussion presented by Wilson, 1937). Because of the difficulties of homologous comparison, the male fructification of *Dolerotheca* may conveniently be referred to by a noncommittal morphologic term as a *campanulum*.[2] Essential features of such a *campanulum* are diagrammatically sketched in text figure 1. The external aspects of *Dolerotheca* fructifications have been reconstructed as shown in the frontispiece illustrations A, B, and C.

Dorsally, that is, on the side of attachment, the organ is enclosed by a differentiated layer here called the campanulary cover; the distal surface is evidently adapted to permit emission of spores from the sporangia. The distal side is covered by a tissue zone, here called the dehiscence layer, although no kinetic mode of sporangial dehiscence has been recognized. The dehiscence layer is more or less radially grooved and each ripened sporangium opens by a slit or pore into the grooves of the distal surface. There is evidently no analogue of the prismatic epidermal cells so common in sporangia of cryptogamic plants which frequently are specialized to provide for expulsion of spores.

The dehiscence layer probably is perforated when the campanulum dries at maturity. It may be that radial tensions are set up at that time to cause rupture of this layer at the distal ends of sporangia. In any event although the sporangia are completely immersed in parenchymatous and sclerotic intrasporangial tissue, the tips are effectively opened to shed the spores. No instance has been observed where an isolated sporangium has failed to open so that the full normal and mature complement of spores was still retained. In the *Dolerotheca* campanulas described by earlier authors, more numerous spores apparently were retained in the sporangia, but their specimens were so incomplete or unfavorably preserved that dehiscence details could not be reported.

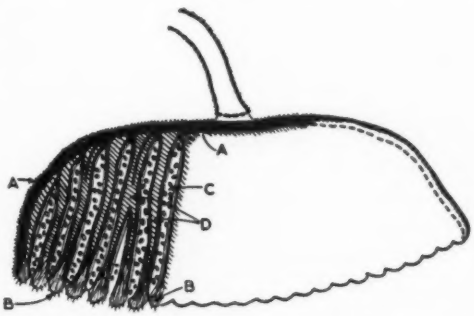


FIG. *1*—The campanulum of *Dolerotheca*. Median longitudinal aspect: Diagrammatic
A. Campanulary cover layer
B. Dehiscence layer
C. Tubular sporangia
D. Inter-sporangial tissue: ground parenchyma, secretory elements, sclerenchyma, vascular strands.

The sporangia are in paired rows radiating from the center of the fructification, with their long axes approximately parallel to the organic axis of the campanulum. New double rows of sporangia are intercalated towards the periphery of the solid bell-shaped structure.

Glandular pubescence is a common attribute of many pteridosperms and has been

[2] Refering to the external form; *campanula*, L., a little bell.

EXPLANATION OF PLATE 105

FIG. *1*—*Dolerotheca formosa*, transverse section of fructification at level of dehiscence tissue. From coal ball 129 A (t 7).

2—*D. formosa*, longitudinal section of fructification showing shorter sporangia at margin; note slight sigmoid curvature of longer sporangia. A transverse section of *Alethopteris* leaf is shown at the bottom below dehiscence tissue. From coal ball C 1 B 1 (b 18 c), magnification same as figure *1*.

3—Vascular strand from section shown in figure *2*. Tissues around it are poorly preserved; at the left is tissue bounding a sporangium.

4—Vascular strand shown in figure *3* but at higher magnification showing scalariform and spiral elements.

discussed by Halle (1929, p. 21–22) relative to seeds, and also was described by him (Halle, 1933) on the male fructifications of *Goldenbergia*. Relatively dense short hairs are present on the campanulary cover of *Dolerotheca*, and more sparse longer hairs on the epidermis of the dehiscence layer. Their function, if they possessed a function, is not apparent, but they seem suitable for use as taxonomic criteria. Hairs also are present on the surface of the *Codonotheca* male fructification, one other genus included in the Whittleseyinae.

The spores produced by the campanulary fructifications of *Dolerotheca* are very large, sometimes longer than half a millimeter, or as much as 10 times the usual dimensions of isospores or microspores of cryptogamic plants. They tend to be considerably larger than the pollen grains known from fossil cycads and conifers. They are, however, more primitive in organization than true pollen grains and it seems evident they are more advanced than cryptogamic microspores. For this reason it seems desirable to refer to the spore bodies of the dispersal stage as prepollen, following the practice long ago adopted by Renault (1893–96).

The size of the prepollen and the organization of the campanulas that bore them, immediately suggests a considerable biologic problem regarding the means of effecting fertilization. Such large heavy prepollen obviously was not well adapted to ordinary wind pollination, as the pollen of many modern plants is. Insects have been suggested as a possible vector agent for fertilization but there is little positive evidence to support this idea beyond the mere presence of glandular pubescence which might have attracted insects. To carry this sort of prepollen effectively the insects should have been of a specialized type.

Plants with this kind of prepollen had a relatively long span of geologic existence. The prepollen grains are commonly found in many Upper Carboniferous coal beds both in America and in Europe.

Thus there is good reason to believe that fertilization actually was accomplished with relative ease, because otherwise the plants could not have been as extensively distributed; at times they were certainly dominant elements of the vegetation. Indeed, Andrews (1945, p. 332) has inferred from his study of their stem anatomy, that Medullosans may have grown in rather dense stands. The prolific occurrence of *Medullosa* stems and roots, *Myeloxylon* type petioles, *Alethopteris* type foliage, *Rotodontiosperm* seeds, and *Dolerotheca* campanulas at the one locality which provided two of the species described below, tends to support this view. However, no evidence points directly at any one of the modes of fertilization suggested by Halle (1933, p. 51). Certainly *Dolerotheca* has the most massive male fructification of any groups Halle included in the Whittleseyinean subtribe, and if the prepollen was expelled by gusts of wind as a general occurrence in smaller forms such as *Goldenbergia* or *Boulaya*, a gale might have been required to clear the spores from sporangia of the massive campanulas of *Dolerotheca*.

Although a majority of spores evidently had been shed in most specimens observed in this study, a number of prepollen grains persist in some sporangia of most of the specimens. It appears to be a reasonable inference that the emission of spores through the distal sporangial opening was often not complete. In spite of obvious maladaptation for easy spore distribution, the writer is inclined to favor dissemination of prepollen by strong gusty wind as more inherently probable than distribution by insects or similar agents. The prepollen is obviously more protected from contact with small vagrant animals than it would be from the mechanical effects of sporadic air currents. There can be little question that intermittent winds could have dislodged most of the prepollen and carried it a little distance after it left the sporangial openings. Information about the location of campanulas and seeds on the parent plants is not sufficiently clear to formulate any opinion as to how far the fertilizing elements would need to be transported after they left their sporangia in order to effect fertilization.

The more important and demonstrable features discussed above are used to establish a new group, parallel to the Whittleseyinae in nomenclatural status. It is clear that *Dolerotheca* differs in some important features from those shown by the Whittleseyinean group. It is believed that coordinate taxo-

nomic ranking of the Dolerothecinae will assist in unifying information about the various genera typified by diverse fossil specimens, so that they can be brought together more easily into a "normal" familial group. In the future it is hoped demonstrated characteristics of the Medullosaceae will come to compare favorably in all essentials with those of families chiefly based on modern material.

Subtribe DOLEROTHECINAE Schopf. n. subtr.

Diagnosis.—Plants of Medullosan alliance possessing massive male fructifications enclosing numerous elongate tubular sporangia. Sporangia paired in rows radially disposed, containing exceptionally large spores of the prepollen type. Prepollen grains oval, not quite bilaterally symmetrical, with a linear proximal suture. External surfaces of fructification characteristically pubescent.

Type genus.—*Dolerotheca* Halle.

The Dolerothecinae is distinguished from the Whittleseyinae by the massive campanulum, and the more numerous and differently disposed sporangia. It is distinguished from the Potoniéinae by the character of its prepollen, and possibly by features of the sporangia that are not as clearly defined at the present time. *Heterotheca* of the Lower Carboniferous, which may well represent an allied ancestral group, is to be distinguished by lack of tubular sporangia, by differences in its spores, and its smaller size.

Dolerotheca is at present the only genus assigned to the Dolerothecinae. The material available now enables a more satisfactory generic diagnosis to be presented. Although certain features of the genotype species thus acquire added significance, it does not seem that any change in taxonomic meaning "circumscription" is involved, and therefore, although the diagnostic description of the genus is somewhat amplified, it is not regarded as emended.

Genus DOLEROTHECA Halle.[3]

Amplified Diagnosis.—Plants agreeing with the Dolerothecinae (see above), with male fructifications externally campanulate or broadly campanulate in form, enclosing tubular sporangia completely immersed in the campanulary tissue. Sporangia paired in biseriate rows, with additional double rows of sporangia intercalated toward the margins; order of sporangial maturity probably slightly gradate and trending centrifugally. The cover of the proximal side of the campanulum bearing a glandular pubescence of short hairs; distal dehiscence surface with more sparse and more slender hairs and epidermal papillae.

Type species.—*Dolerotheca fertilis* (Renault) Halle.

Halle restudied as much of Renault's material of this species as could be found in

---

[3] Whether *Dolerotheca* is a valid name or not, is open to some question. One of the results of this study has been to show that the specimen and counterpart Grand 'Eury illustrated and described under two generic assignments in 1890, i.e., *Androstachys* in textual description, *Discostachys* for the plate, is congeneric with the present *Dolerotheca* material. Grand 'Eury's specimen is evidently a reasonably well preserved compression example of the type that may be more commonly recognized now that it is possible to interpret the structure.

Halle in 1933 was unable to be sure of the generic identity of the Grand 'Eury specimen and that shown by Renault's silicified fragment of *Dolerophyllum fertile;* the latter was taken by Halle to be the generotype of *Dolerotheca*. The present material is complete enough to show clearly that the *Androstachys-Discostachys* specimen and the silicified fragment are congeneric. The popular old name "Dolerophyllum," which Renault used in the sense of a combination genus, is of course inapplicable to the fertile specimens that had been included in it, as Halle recognized. But we cannot now regard the *Androstachys-Discostachys* specimen as ambiguous, as Halle suggested. One would suppose that one of the names proposed by Grand 'Eury, either *Androstachys* or *Discostachys*, would have to be applied since both have a clear claim to priority over *Dolerotheca*. White, in fact, anticipated this possibility in 1903 and suggested, with reference to some comparable material that *Androstachys* should be selected "if the generic identity of the sterile leaves (i.e., referring to *Dolerophyllum*, s.s.) and the supposed polleniferous leaves is not established."

The name *Androstachys* is, however, unavailable since Grand 'Eury himself had used the name earlier in reference to a fertile zygopterid frond. Therefore *Androstachys* Grand 'Eury, 1890, is a junior homonym of *Androstachys* Grand 'Eury, 1877, and though now regarded as a synonym, such names cannot be reused according to the express stipulation of Article 61 of the International Rules of Botanical Nomenclature.

1929, and presented the results of his observations and new photomicrographs in 1933. A line tracing from the transverse section Halle studied, showing arrangement of sporangia, is reproduced here in text figure 2.

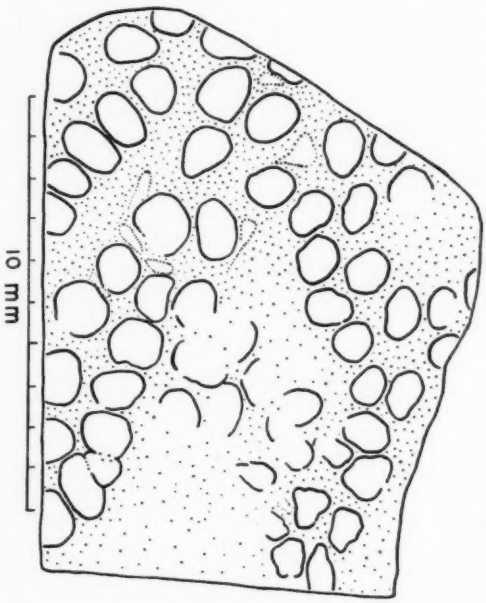


FIG. 2—*Dolerotheca fertilis*, transverse section of Renault's holotype. Line tracing from published photograph by Halle (1933, pl. 9, fig. 2), showing about 50 sporangia, most of which are associated in paired rows.

It is evident that it accords with species described below in having radially paired rows of sporangia. This interpretation is more in agreement with Halle's alternative suggestion (Halle, 1933, p. 48) and with the structure shown by the "Mont-Pelé" compressions of *Dolerotheca*.[4] A photograph of a longitudinal section of *D. fertilis* was illustrated lithographically by Renault in a little known publication in 1902. This figure (Renault, 1902, Pl. 115, fig. 1) has been rephotographed and is presented in pl. 104, fig. 8 for comparison. Three additional figures of prepollen have been copied from this same publication by Renault (1902, pl. 114, fig. 4, pl. 12, figs. 3–4) and are reproduced in pl. 108, figs. 11–13. All the structures are in evident generic agreement with the new forms described below. The most divergent structure is the ground parenchyma, described as aerenchymatous by Renault, but scarcely mentioned by Halle. Sclerenchyma seems to have been lacking in the European forms.

NEW SPECIES OF DOLEROTHECA

Three new species of *Dolerotheca* are described below. The writer has had the opportunity to examine the holotypes of all three species, and has made thin sections of the specimens. Two of the species are from the Mont-Pelé locality, and the third is from the Autun basin.

There seems no alternative to the conclusion that *Discostachys* Grand 'Eury, 1890, type *D. cebennensis*, as illustrated by that author in plate 7, fig. 2 A and A', in the Gard report, is a name that may be available, with priority over *Dolerotheca* Halle, 1933. If the name had not been confused with *Androstachys* and if a proper description had appeared under the name *Discostachys* no question would exist about the propriety of using it in this connection. Grand 'Eury for inexplicable reasons confused the names he applied to his specimen but the descriptive facts pertinent to it are relatively clear. The chief problem now is to properly incorporate this information systematically.

So far as factual matters pertaining to identification are concerned, it does not make much difference which name is applied. The nomenclatural types of both names leave much to be desired in the way of completeness and preservation. The writer believes, however, that preference should be given to *Dolerotheca*, although it was proposed later. It is a name now in current use, being mentioned in at least three recent textbooks. *Discostachys* is in complete disuse, apparently has never been cited in a textbook, and was regarded as a dubious and confused synonym by both White and Halle. Hence, in the present paper the writer proposes to retain *Dolerotheca* as Halle introduced it in 1933. In order to clear it of conflict with *Discostachys* G. 'E., 1890, he further proposes that *Discostachys* be regarded as a *nomen confusum* and that *Dolerotheca* be added to the list of officially conserved names, being specifically conserved over *Discostachys* as typified by *D. cebennensis* G. 'E., 1890.

It appears to the writer that this course is the one most likely to promote stability in reference to the group of plants involved. Any other is likely to lead to prolonged nomenclatural confusion that would be profitless in advancing knowledge of these plants or any aspect of paleobotany.

[4] Saporta and Marion (1885, p. 74) also mention that locules of the "Dolerophylleae" (evidently they had the Mont-Pelé specimens described as *D. berthieri* in mind) are distributed in "two contiguous rows."

scribed below. One of them, distinguished as *D. formosa*, is represented by a somewhat indefinite number of specimens. They are rather common in the large coal ball aggregate collected from a coal bed below the Calhoun limestone in southwestern Richland County, Illinois, in 1937. A preliminary note (Schopf, 1938) identified the zone as lower than the La Salle limestone, but it has been learned since that this was in error and that its stratigraphic position is higher. The deposit is in the upper part of the McLeansboro group and has been discussed relative to other coal ball zones in a previous publication describing an unrelated lycopsid form, *Mazocarpon oedipternum*, that was found in the same coal ball aggregate (Schopf, 1943). A considerable number of the *D. formosa* fructifications are quite fragmentary. Study has has been mainly based on three essentially complete specimens. About 15 other specimens in a good state of preservation have been observed incidentally in slices of the Calhoun material, and the general features have been checked from them, both on sawed and etched surfaces and from peel preparations.

Two specimens of a much smaller form, here described as *Dolerotheca villosa*, also were discovered in examinàtion of coal balls from the same deposit.

The third species has been described under the name of *Dolerotheca reedana*, so called in recognition of Fredda D. Reed, Professor at Mt. Holyoke College. Professor Reed discovered this specimen in the course of her investigation of fossil plants in coal balls from the Harrisburg (No. 5) coal bed in Saline County, Illinois. She generously permitted the writer to include it in this study when it was learned that comparable material from the Calhoun locality was being investigated. *D. reedana* thus is from the Carbondale group of the Illinois Pennsylvanian, and of considerably earlier geologic age than the other forms described here. At present it represents the oldest described species of *Dolerotheca*, but future discoveries will probably extend the range of the genus into still lower strata.

The most obvious difference between the three species is in size and character of pubescence, but other differences also can be noted.

DOLEROTHECA FORMOSA Schopf, n. sp.
Frontispiece, figures A, B; plate 104, figures 1–7; plate 105, figures 1–4; plate 106, figures 1, 2; plate 107, figures 1–6; plate 108, figures 1–10; text figures 3a–d, 4–13

External Characters.—Male fructification broadly campanulate, about 40 mm. in diameter and 11–14 mm. thick. Point of attachment somewhat excentric. Proximal (dorsal) side convex, probably of leathery texture, somewhat irregularly indented radially, indentations diminishing toward margin. Proximal surface covered with numerous glandular simple hairs, sometimes capitate tipped. Distal side also slightly convex, with bifurcating radial (dehiscence) grooves 1–2 mm. deep except near the center where they become obsolete or less regular. Sporangia are arranged in double rows between the grooves and open into them by slit-like perforations. Toward the center of the fructification sporangial openings are more pore-like since the grooves are shallower there. Distal surface covered with sparse simple hairs and epidermal papillae; the hairs consist of one to three cells and are more slender and much less glandular appearing than those on the proximal surface.

An accurately scaled reconstruction of these external features is presented in the frontispiece figures A and B. The peduncle only, in fig. A, is hypothetical since no attached specimens have been found. The proportions of these figures have been carefully checked with sections in both planes.

General Anatomy.—The tubular sporangia of *D. formosa* are 0.6 to 1 mm. in diameter and vary from about 4 to 12 mm. in length. In a preliminary note (Schopf, 1938) they were described as "radially related in pairs of rows; sterile locules alternate with the fertile ones in each radial series." This is a fair statement of the arrangement of sporangia and other cavities but the "sterile locules" mentioned should be designated by the more non-committal term, lysigenous tubes, because there is no evidence of their sporogenous nature although this at first seemed probable. The tissue surrounding the lysigenous tubes is ragged on all edges. Aside from miscellaneous tissue frag-

ments none has any contents. They may function as respiratory chambers somewhat as the parichoi of lycopod stems, although there seems to be no special means of communication with the exterior. Renault thought the aerenchymatous tissue of *D. fertilis* would assist the fructification to float in water. Doubtless this suggestion would apply as well to the lysigenous cavities, but the advantage of this structure is not evident unless the plants had the growth habit of pond lilies—a suggestion which for various reasons seems far fetched.

Relations of the sporangia are diagrammatically illustrated in text figure 3. The outer dark shaded zone represents the campanulary cover which in this species is about 400–800 μ thick, and extends over the strongly convex proximal surface as shown in figure 3d. The double rows of sporangia are best shown in cross-section close to the lower dehiscence surface (fig. 3 c). This surface is covered by an epidermis beneath which appears the rather delicate elongate cells of the dehiscence tissue. The dehiscence tissue covers the lower ends of the sporangia and the areas between. It extends deeper inside the fructification along the strong dehiscence grooves as shown in the frontispiece figs. B. Thus a section across this lower part of the fructification (fig. 3 c) shows the free sides of sporangia clothed by the dehiscence tissue which has split opposite each locule to provide egress of spores from sporangia. The lower surface of these fructifications is slightly convex so that the section shown in text figure 3 c is slightly off the main transverse plane, more accurately transected by the section shown in text figure 3 b. Near the margin of this figure the dehiscence tissue and grooves between the sporangial rows again are shown. Centrally the sporangia are tubular and separate except where septae have broken down. Text figure 3 a, from a section across the middle of the fructification, shows a very similar character although the double rows are not so obvious. A nearly radial longitudinal section is shown in text figure 3 d and the transverse planes corresponding to the sections in figures 3 a–c are approximately indicated.

One of the interesting features in arrangement of sporangia is the way new paired rows are added by intercalation toward the margin. Text figure 3 c shows this best by the course of the dehiscence grooves. Plate 105, figure 1 represents a photograph of part ofthis same section. In the longitudinal plane the sporangia incline upwards around the margin of the fructification as shown in plate 105, figure 2 until they abut on the dorsal cover layer. Thus they are shorter than sporangia more centrally located. This feature may provide a clue to the mode of growth of these fructifications. It also is worthy of note that many of the sporangia are not actually straight but have a slight sigmoid curvature which is apparent in nearly all of the near-radial sections (text fig. 3 d; plate 104 figs. 1 and 2; plate 105 fig. 2; plate 107, fig. 1).

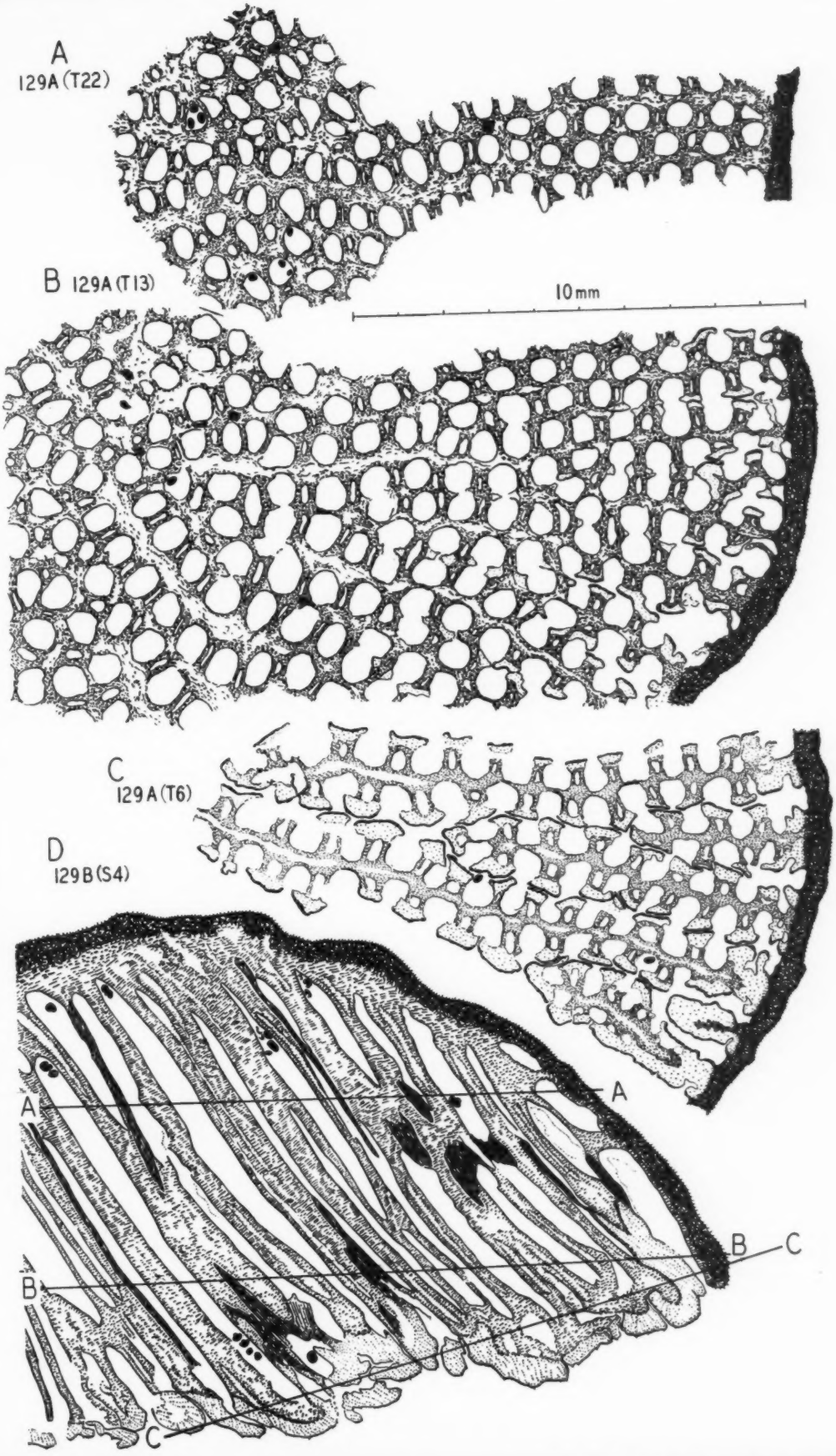
In regard to growth the chief question is the order of sporangial maturity, whether centripetal or centrifugal. One would expect the sporangia first formed in ontogeny to be the most complete and longest. These evidently are the ones centrally placed in this fructification and so it seems most plausible that the fructification expanded as a capitate head with the central, i.e., the most axial sporogenous tissues maturing first and marginal tissues somewhat later. The course of maturation in this event would be centrifugal or opposite to that in umbels and capitula of modern plants. The number of marginal rows produced and the final diameter attained by the fructifica-

---

FIG. 3—*Dolerotheca formosa*, sections of fructification: schematic indication of tissues. Spores are shown black, inter-sporangial tissue (ground parenchyma and sclerenchymatous strands) represented by dashed areas, dehiscence tissue is stippled, campanulary cover dark with white stippling. Drawings prepared by projection of "peel" sections at low magnification, scale of enlargement is indicated. The serial number of preparations is given for each figure.

A, B, C.—Transverse sections.

D.—Vertical (slightly tangential) section. Ruled lines (A–A, B–B, C–C) indicate approximate relative levels at which transverse sections for figures A, B, and C were obtained; the transverse series is from a different specimen than section D; both are from coal ball 129.


A
129A (T22)
B 129A (T13)
10 mm
C
129A (T6)
D
129B (S4)
A
A
B
B
C
C

tion was probably dependent to some extent on environmental conditions which favored or retarded growth and reproductive processes in the plant.

Histology.—The proximal or dorsal side of the fructification is covered by the rather thick more or less coriaceous campanulary cover. It has a definite cuticularized epidermis bearing numerous short glandular appearing hairs. These hairs are 60–90 μ long and about 45 μ broad consisting of from two to five cells, all of which except the terminal cell are broader than long. The terminal cell is variously cone-shaped and sometimes has divided into two cells to become capitate. All the cells have dark contents shrunken away from the cell walls, which gives the hairs a glandular appearance. The dark material does not appear "resinous" and may be the remains of a dense cytoplasm containing tannin derivatives or other materials. Some cells contain rounded central bodies reminiscent of nuclei. Three of the hairs are shown sectioned vertically in text figure 12. A somewhat better idea of the hairs and epidermal pattern is obtained from cuticular fragments prepared by dissolving the calcite matrix in dilute hydrochloric acid. The hairs drawn in outline in text figure 9 a were obtained in this way and the arrangement of cells around the hair bases is shown from a similar preparation in text figure 9 b. Photographs of the same material are shown in plate 107, figures 3–5. Figure 5 was taken at a higher plane of focus than the others to show the upstanding tips of the hairs. These fragments prepared by hydrochloric acid treatment have the advantage of being more translucent than thin sections since much of the dark cell contents has been removed. The epidermal cells proper are irregularly polygonal with contents similar to that of the hairs. The dark contents are not limited to the hairs and epidermis but several layers of deeper cells near the lower margins of the fructification also possess similar inclusions as shown in text figure 7. From two to four or five cells may adjoin the basal hair cells. No stomates have ever been recognized in the epidermis of the cover although, in view of the spongy tissue lower in this layer, their absence is noteworthy.

Beneath the epidermal tissue is a zone of spongy parenchyma generally not well preserved, with numerous large intercellular spaces. Isolated in this spongy tissue are groups of nearly isodiametric sclerotic or stone cells. These are shown most clearly in the section illustrated in plate 107, figure 6, which was cut obliquely tangential to the cover layer and appears thicker than it actually is for this reason. The groups of stone cells seem comparable in position to the sclerenchyma of the sparganum cortex of *Myeloxylon* petioles and also to cells of the sclerotesta of certain trigonocarp seeds. The cell shapes and the tissue occurrence differs considerably, however, so that the histologic similarities are not very marked. Numerous large secretory canals are also present and possess characteristic opaque contents. The contents often are more broken by calcite intrusions than the resin rodlets[5] of *Myeloxylon* petioles. This may indicate that the contents in the two instances were somewhat different in consistency and perhaps slightly different in composition when mineralization occurred.

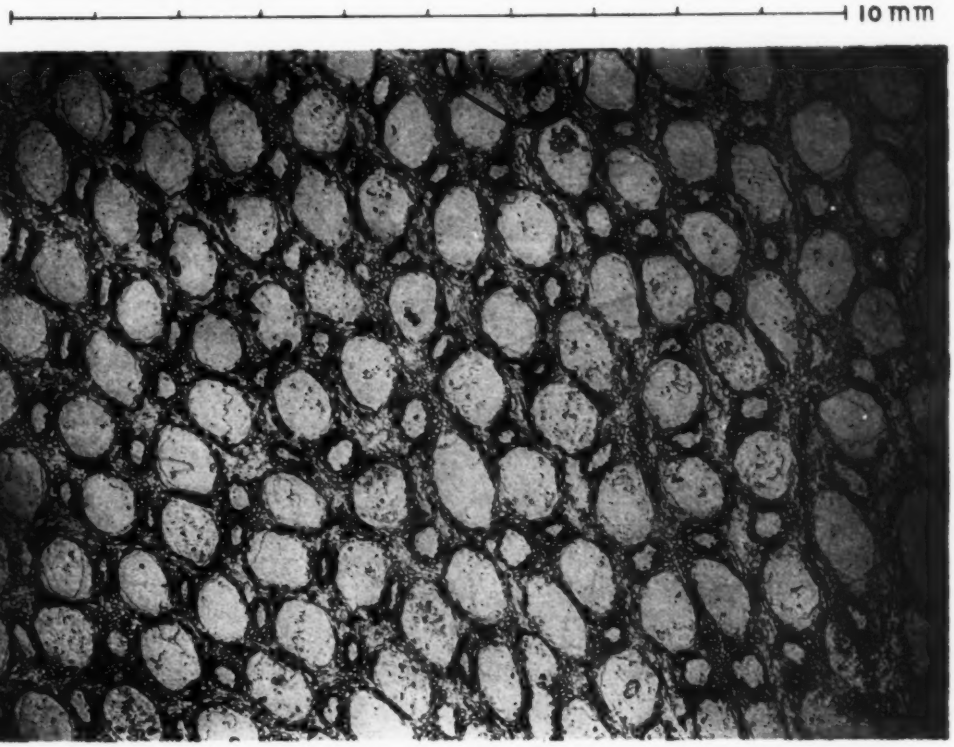
The vascular supply of the campanulum of *D. formosa* is not prominent. It has never been possible to demonstrate tracheids in the marginal region. In a few instances delicate strands of small closely spiral, annular or scalariform tracheids have been seen near the top of the fructification. These are generally located internally at a lower histologic level than either the secretory canals or the groups of stone cells and are appar-

[5] The term "resin rodlet" is used herein only in a descriptive sense similar to the usage in coal microscopy. In no case is any particular chemical composition to be inferred from the descriptive use of this term.

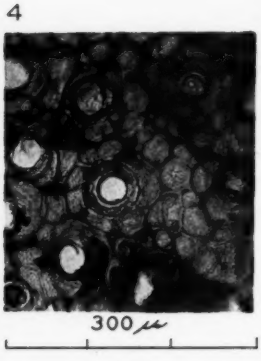
EXPLANATION OF PLATE 106

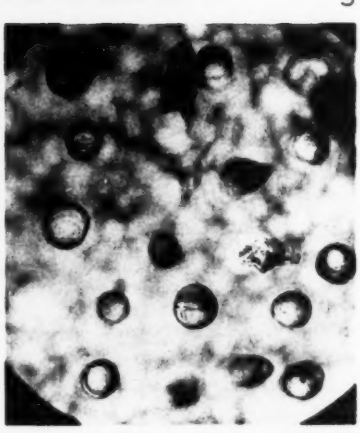
FIG. *1*—*Dolerotheca formosa*, transverse section near center of fructification about 3 or 4 mm. above level of dehiscence tissue. From coal ball 129 A (t 12).

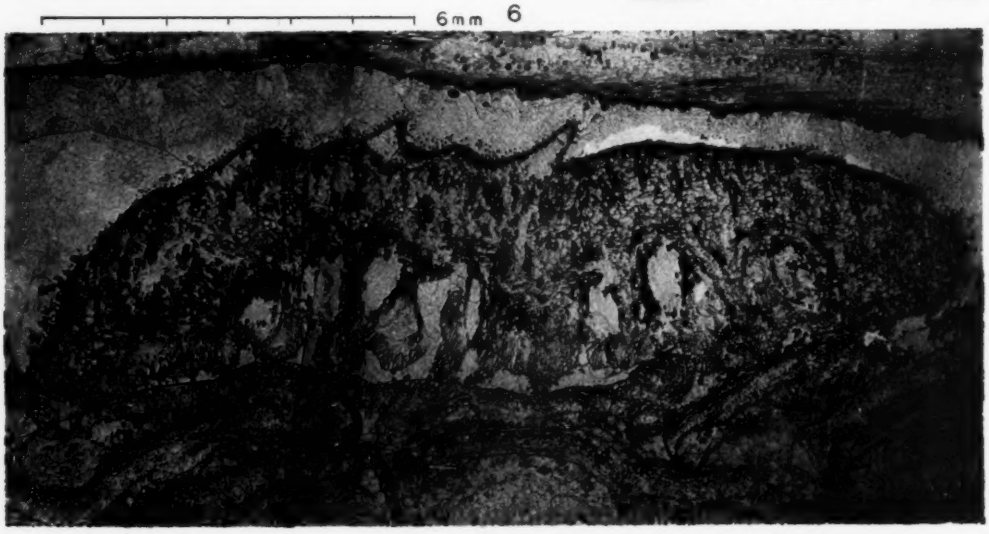
2—Section similar to figure *1* but about 3 mm. higher, showing more compact structure. From coal ball 129 A (t 27), magnification same as figure *1*.



Schopf, *Dolerotheca formosa* n.sp.







Schopf, *Dolerotheca formosa* n.sp.

ently unrelated to either in their position. Presumably phloem accompanies them but preservation of the tissue immediately surrounding them is poor and the details are obscure.

The spongy tissue of the cover merges internally with the intersporangial ground parenchyma which is somewhat thicker walled, has larger cells and is generally well preserved. The cells tend to be radially elongated as is apparent in the longitudinal section in text figure 5, and in the transverse sections illustrated. The intersporangial parenchyma is the fundamental groundwork of the fructification, since it chiefly encloses and in fact often seems to constitute the walls of sporangia. A relatively small number of cells, chiefly in the lower part near the dehiscence area, possess secretory contents. The ubiquitous resin rodlets also occur in this ground parenchyma and extend down close to the dehiscence surface (cf. r. r., text fig. 6).

Although ground parenchyma appears to constitute most of the wall of the sporangium without any sort of differentiation, in many sporangia there is a somewhat shrunken membrane which originally enclosed the spores. This membrane is noncellular and does not seem to be of waxy nature like cuticle although it is quite persistent. That it is an organic structure and not a pseudomorph in the calcite is shown by its presence as a definite membrane in nitrocellulose peels. There are at least two possible explanations for this membrane. One is that it represents the remains of a sporangial plasmodium. However it might better be taken to represent the remains of peri-archesporial tissue which has been transformed to a gelatinous or mucilaginous film. The latter is more probable because it seems the ground tissue must have shown some differentiation adjoining the sporangia, at least during the early stages of growth. Since differentiated perisporangial tissue is not otherwise in evidence, the sporangial membrane probably represents a vestige of it.

The dehiscence tissue occurs over the distal ends of sporangia, extending up above the radiating dehiscence grooves. It consists of undulated elongate cells with oblique and tapered end walls. Cells near the distal surface are thin-walled and from three to five times as long as broad (cf. text fig. 9 c). Deeper within the fructification the cells become longer, more tapering at the ends, and their walls thicker and straight. In short, they assume all the characteristics of fibrous sclerenchyma. Although they merge in this manner with the internal sclerenchyma system (described on p. 696) only the thin-walled tissue has contact with sporangial openings. It is not assuredly established that specialized kinetic cells are nowhere present to provide for the opening of sporangia, but they have not been recognized and no dehiscence mechanism is evident.

So far as can now be ascertained, spores are shed through slits or pores produced by mechanical fracture of the dehiscence tissue. It is not altogether clear why the fractures always coincide with the distal ends of sporangia. Since no actually "motivating" cells responsible for the opening of sporangia can be demonstrated, the designation "dehiscence tissue" may not be particularly appropriate; still it appears that this thin-walled tissue is specially modified as a whole to permit shedding of spores. In any

---

EXPLANATION OF PLATE 107

FIG. *1*—*Dolerotheca formosa*, longitudinal section similar to fig. *2*, Pl. 2. Note dark sclerotic strands which merge below with the dehiscence tissue. From coal ball 219 C 1 B 1 (b 9), magnification same as fig. *6*.

2—*D. formosa*, intersporangial vascular strand. From coal ball 219 C 1 B 1 (b 18).

3, 4—*D. formosa*, cell patterns of proximal cover epidermis showing frequency and relative position of hairs. From hydrochloric acid maceration of coal ball 229 B 2 C.

5—Same as above, photo at higher plane of focus to show the tips of upstanding hairs. Note hair broken from its base; hairs similar to these are the basis of drawings in text fig. *9* A.

6—*D. formosa*, longitudinal section at margin of fructification. Note groups of sclerids in the cover layer and hairs shown above it. The hairs appear disconnected because the section is oblique with reference to the surface of the fructification. From coal ball 219 C 1 B 1 (b 44).

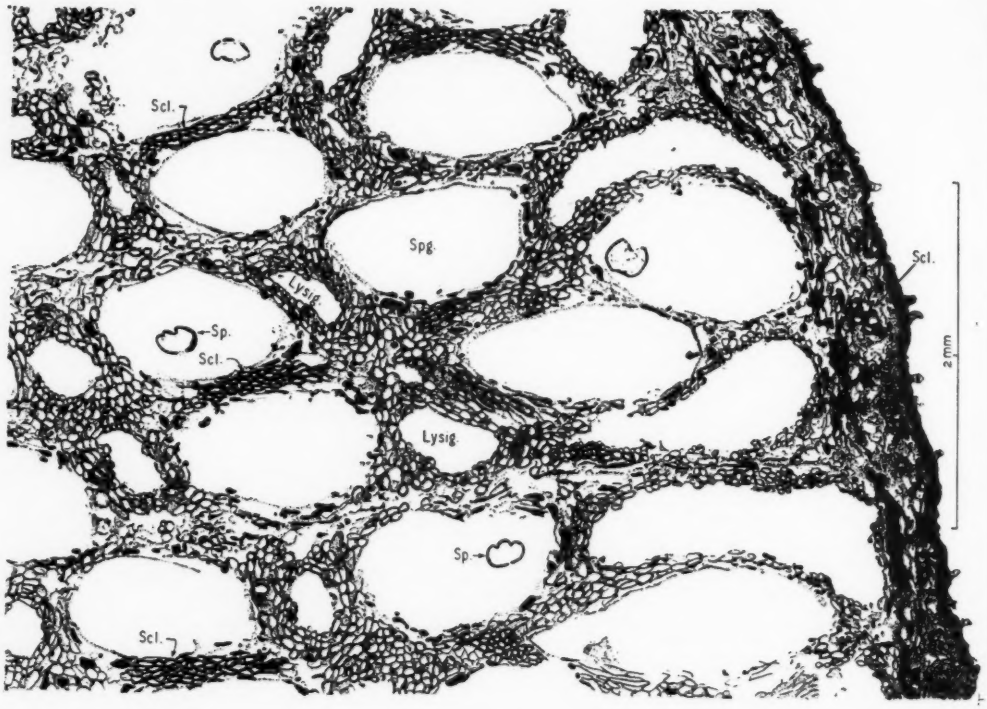


FIG. 4—*Dolerotheca formosa*, transverse section showing spores (Sp.), sporangia (Spg.), lysigenous tubes (Lysig.), Sclerenchyma (Scl.). The character of the inter-sporangial tissue and of the campanulary cover also is shown. From coal ball 129 A (t 37).

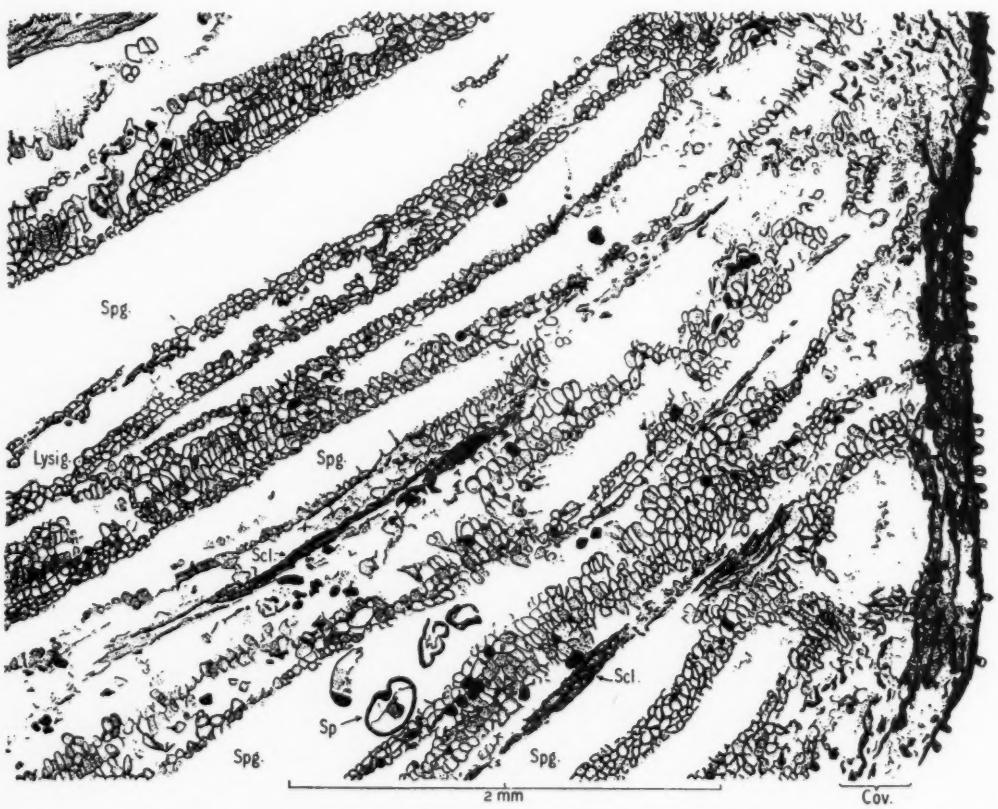


FIG. 5—*Dolerotheca formosa*, longitudinal section for comparison with transverse section shown in text figure 4 (lettering symbols the same; cov. = campanulary cover). From coal ball 129 (B_3).

event this function is the essence of sporangial dehiscence, whether by a kinetic mechanism or not. Sections across the slits in the dehiscence tissue communicating with sporangia are shown in text figs. 7 and 8. The preservation is best in marginal areas such as shown in fig. 7 and this also may indicate that maturation of the fructification proceeded centrifugally. If the central as the dehiscence tissue opposite the ends of sporangia. No stomates have been observed but it is conceivable that the dehiscence pores are initiated by some sort of modified stomatal apparatus. The hairs are more sparse than on the dorsal cover surfaces, more slender, simple, consist of 1–3 cells, and are less glandular appearing. No capitate tipped hairs have been observed.

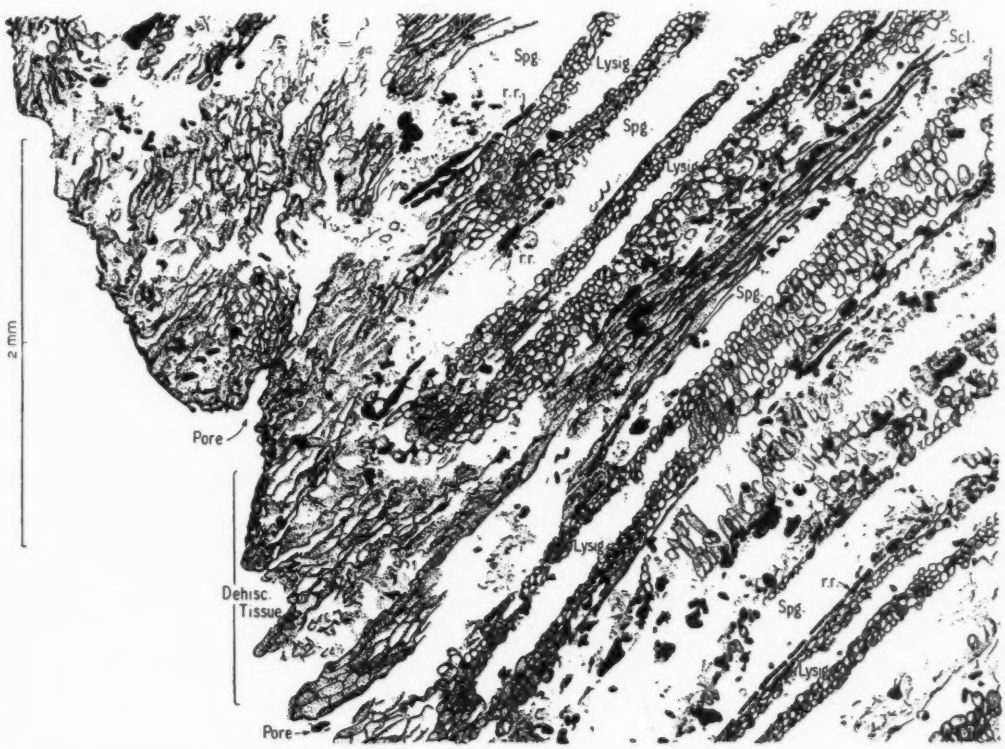


FIG. *6—Dolerotheca formosa*, longitudinal section of distal part of fructification showing dehiscence tissue, sporangial pores, sporangia (Spg.), lysigenous tubes (Lysig.), sclerenchyma (Scl.), resin rodlets (r.r). From coal ball 129 (b 3).

pores were the first to open, presumably they might become more fragmented before the organ dropped from the plant and had a chance to be petrified.

The definite epidermis of the dehiscence layer is of particular interest since no equivalent of the usual prismatic wall of cryptogamic sporangia is present. This epidermis is composed of somewhat flattened cells often bearing hairs or papillae (cf. text fig. 9 c). It apparently is fractured in the same way Papillae however are extended to a variable degree on nearly all cells not otherwise acting as hair bases. The relation of the distal epidermis to the dehiscence tissue is shown in text figure 9 c, and the shape of distal trichomes may be contrasted with those of the integument shown in figure 9a at somewhat greater magnification. The distal epidermis apparently is not strongly cutinized and is more irregular and broken by original fractures. Consequently no suit-

able preparations have yet been obtained by dissolving the calcite matrix. All the details reported have been observed in sections.

Aside from the campanulary cover, supporting tissue of the large fleshy male fructification of *D. formosa* is limited to the fibrous sclerenchyma strands developing above the dehiscence grooves. As mentioned, cells of the dehiscence tissue merge with the sclerenchyma in these areas by a gradual transition. Apparently the fibrous strands act as isolated buttresses or "stays" to prevent distortion as there are no sclerotic bridges between them. Their arrangement is evident in text figures 4 and 6 and they can also be seen in pl. 107, fig. 1, and pl. 105 fig. 2. Two small strands are shown in text figure 10 deeper within the fructification. A type of cell wall thickening sometimes also occurs in the tangential bars on either side of the lysigenous tubes between sporangia. These cells however are not usually elongate and spindle-shaped like the fibrous strands and probably owe their sclerotic appearance to some other cause. The fibrous strands are somewhat compara-

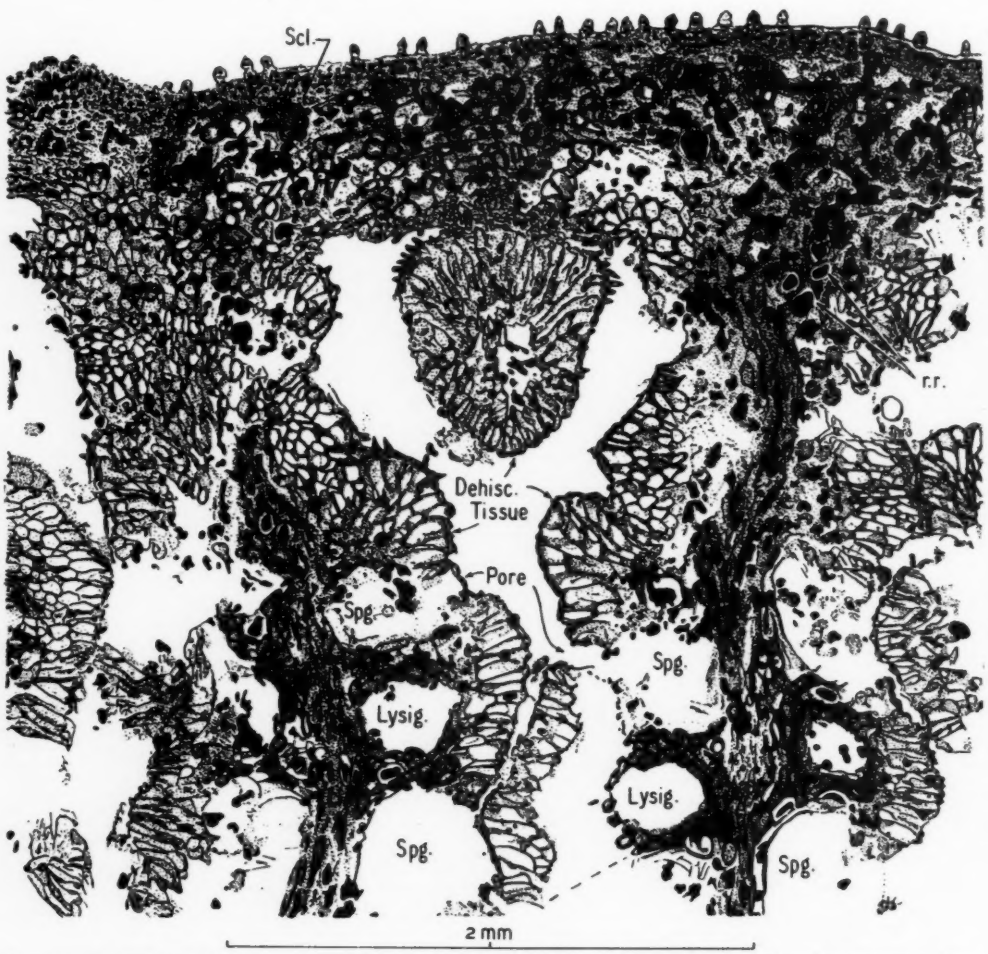


FIG. 7—*Dolerotheca formosa*, transverse section of distal part of fructification showing campanulary cover layer with sclerotic cells (Scl.), dehiscence grooves, dehiscence tissue, sporangia (Spg.), lysigenous tubes (Lysig.) and resin rodlets (r.r.). From coal ball 129 A (t 38).

ble to the sparganum strands of *Myeloxylon* but their distribution is different so that the resemblance may be mostly superficial.

The vascular bundles are noteworthy for their obscurity. They appear to consist of a few spiral or annular tracheids isolated in the ground parenchyma unassociated with resin rodlets or sclerenchyma; they are not numerous. They seem to be restricted to the radii alternating with the sclerenchymatous strands, i.e., *between* the paired sporangia. The ground tissue along these radii is generally rather poorly preserved, perhaps due to a slight difference in its character, and dis-

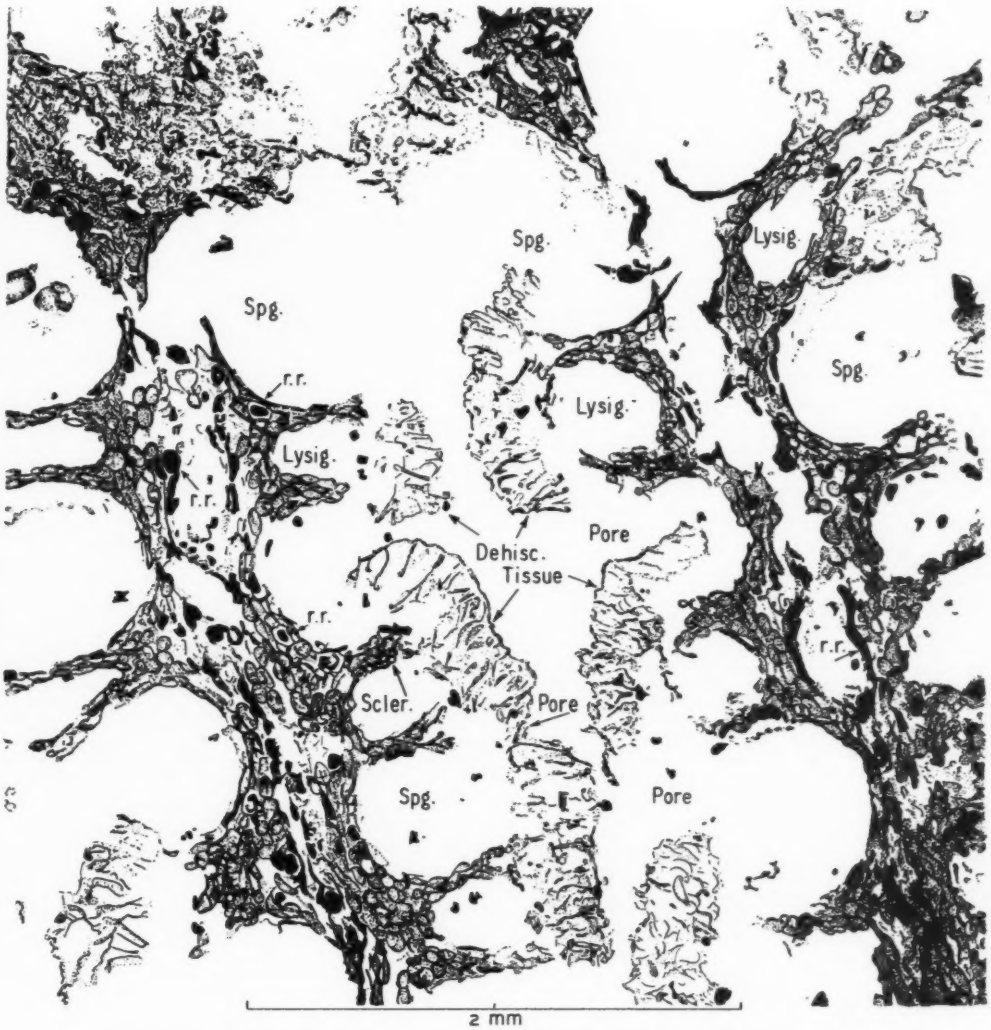


FIG. 8—*Dolerotheca formosa*, transverse section of distal part of fructification more centrally located than text figure 6, (lettering symbols the same). From coal ball 129 A (t 6).

organized humic material is present around all the delicate vascular strands that can be found. The tracheids are very small, average about 15μ in diameter, and can be observed chiefly in longitudinal sections where their annulae distinguish them. Figures

showing the vascular strands are shown in text figure 11 and in pl. 107, fig. 2, and pl. 105, figs. 3 and 4.

The vascular bundles are gathered at the top, always situated rather deep within the cover layer, and branch with bundles penetrating downward between the paired locules. These bundles are hardly comparable in size and character of the elements to those in associated *Myeloxylon* petioles. However they appear to contain elements rather similar to those forming the ultimate veinlets in the *Alethopteris* pinnules, which are abundantly associated with this material. Although fructifications of *D. formosa* are the largest of the *Dolerotheca* species known, they show considerably less vascular development than either *D. villosa* or *D. reedana* described below.

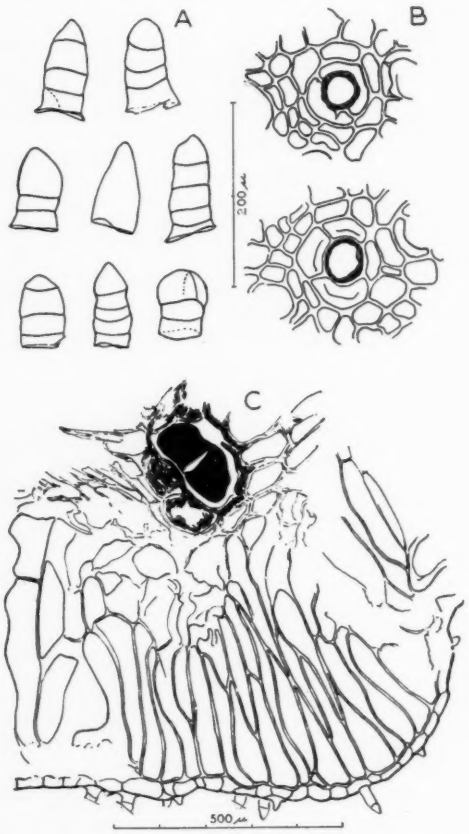


FIG. *9*—A. *Dolerotheca formosa*, hairs of dorsal cover broken from the epidermis after dissolving the calcite matrix.
B. Same, cuticular cell pattern at the base of two of the hairs. Magnification same for A and B.
C. *D. Formosa*, line drawing of dehiscence tissue showing epidermis and hairs. A resin rodlet appears in oblique cross section in the tissue above. From coal ball 219 C 1 b 1 (b 18 c).

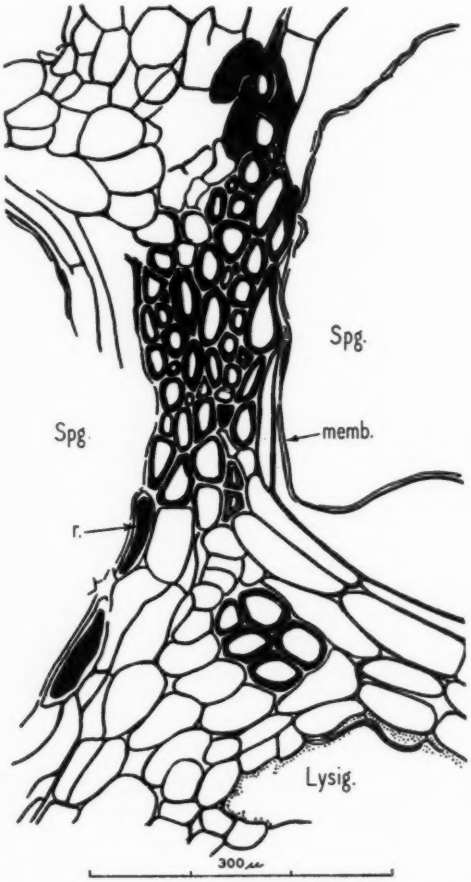


FIG. *10*—*Dolerotheca formosa*, transverse section of a septum with a characteristic sclerenchyma strand between sporangia of opposite paired rows (Spg.), also small lysigenous tube (Lysig.). The sporangial membrane (memb.) is continuous in the sporangium on the right; resinous inclusion (r). From coal ball 125 A (t 25).

Spores or Prepollen.—It is important that the difference be recognized between the preservation of spores in coal balls since

these can be dissolved out undistorted by compression, and those which have been flattened and present a somewhat distorted appearance in coal maceration residues. In the latter, only two dimensions may be accurately observed; the depth dimension must to some extent be reconstructed by inference. In coal ball material all three dimensions may be observed with an accuracy approaching that in living material. Spores of *D. formosa* have been studied isolated after solution of the calcite matrix in addition to those obtained in sections.

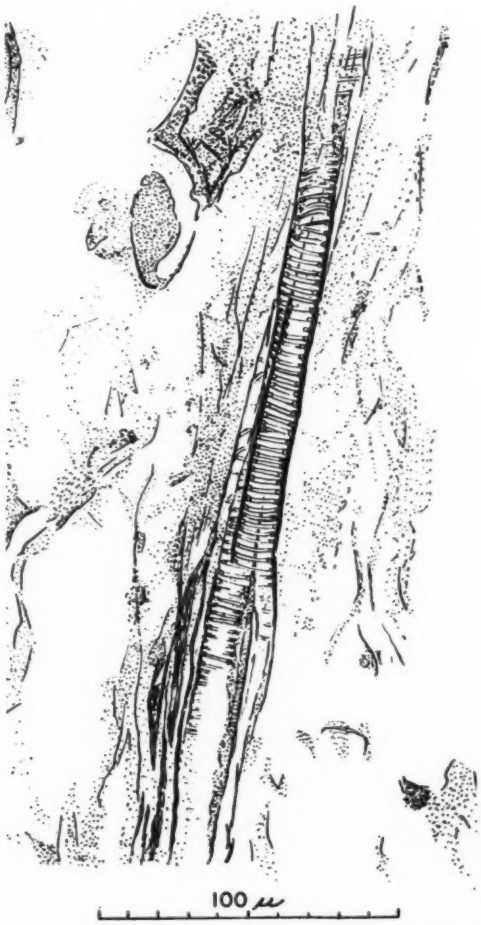


FIG. *11*—*Dolerotheca formosa*, vascular strand from radius of paired sporangial row, showing spiral or annular thickenings. From coal ball 219 C 1 b (b 18a).

Prepollen grains of *D. formosa* are 300–350 μ long and 200–250 μ broad by about 150μ thick. Proximally they are marked by a monolete suture which in nearly all shows a slight angular deflexion near the middle (pl. 108, fig. 7). To the extent that this suture deviates from a straight line, the spores are asymmetric bilaterally. Distally, the coat has two prominent grooves which approach close together at the two ends but are spread farther apart at the center. An

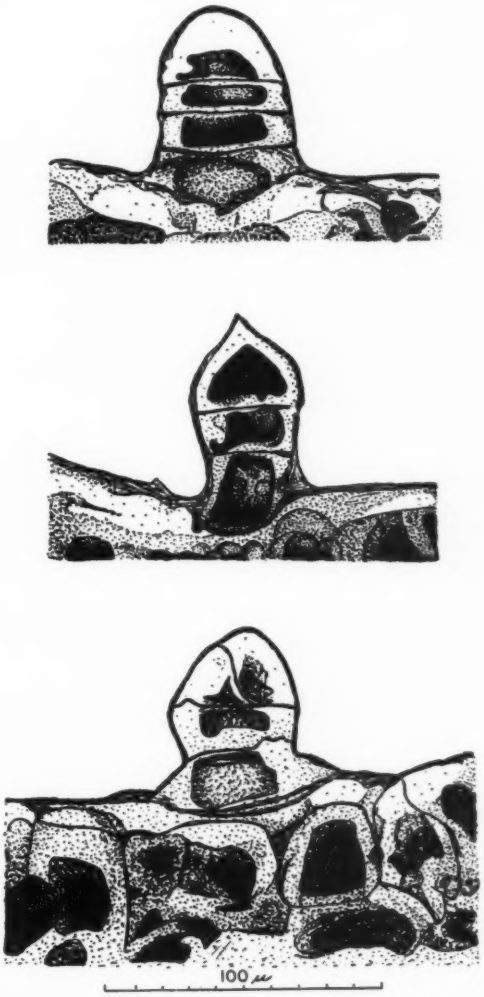


FIG. *12*—*Dolerotheca formosa*, detailed drawing of dorsal hairs and their contents. From coal ball 129 A (t 38).

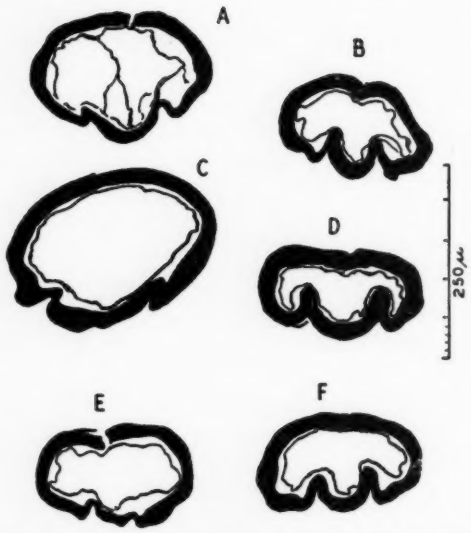


FIG. *13*—A–F. Prepollen or spores of *Dolerotheca formosa*. Outline drawings (microprojection) of specimens still within sporangia, in approximately median transverse section; C is most oblique. Proximal suture is uppermost in each, distal grooves and umbo downward. From peel sections of campanulum in coal ball 129.

almost perfect axial section across the short diameter of a prepollen grain is shown in pl. 108, fig. 4. The distal grooves are uppermost in the figure and the proximal suture is marked by a slight indention at the bottom. Shadow outlines of the distal grooves below the plane of focus are evident in an example isolated by solution of the matrix shown in pl. 108, fig. 6, and in fig. 7 the same spore is illustrated at a higher plane of focus showing the characteristic proximal suture. Figures 8 and 9 of plate 108 show examples of other isolated whole grains where the suture has opened. Median sections across the short dimension of grains are shown in outline in text fig. 13. In no case has the umbo between the distal grooves been found separated as a germinal "operculum," or the distal grooves split, except in irrelevant cases where mechanical disturbance, such as may occur in peeling nitrocellulose films, probably had occurred. The shadow of the distal grooves appears on either side and at a lower plane of focus than the open proximal suture in the whole specimen illustrated in pl. 100, fig. 8. For *Dolerotheca fertilis*, Renault

EXPLANATION OF PLATE 108

Magnification same for figs. *1–9*

FIG. *1*—*Dolerotheca formosa*, spore (prepollen) showing collapse of the exospore (pseudomorph shows original outline) and endosporal membrane shows pseudo-cellular structure due to collapse. Section is obliquely longitudinal and intersects only one of the distal grooves on the lower side. From coal ball 129 C (S 7)

2—*D. formosa*, longitudinal section of spore showing original form of exosporal coat and frayed distorted remnants of the endosporal membrane. From coal ball 129 C (S 7)

3—*D. formosa*, oblique longitudinal section of spore similar to fig. *1* showing pseudo-cellular collapse of endosporal membrane. Small cross composed of pyritic crystals is above the indention caused by one of the distal grooves. From coal ball 129 C (S 7)

4—*D. formosa*, transverse section of spore showing typical configuration of layers of the spore coat. Proximal suture (pr. sut.) is at the bottom somewhat obscured by thickness of the section. dist. gr.—distal grooves; endo—endosporal membrane.

5—*D. formosa*, transverse sections of two spores showing distal contour and proximal sutures (pr. sut). The proximal side of the lower spore is slightly collapsed in preservation similar to that shown in fig. *1*. Dist. = distal umbo. From coal ball 129 C (S 7).

6—*D. formosa*, isolated spore showing outline of slightly collapsed endosporal membrane. Note shadow outline of distal grooves. From hydrochloric acid maceration of coal ball 229 B 2 C.

7—Same as above but at a higher focal plane to show the proximal suture.

8—*D. formosa*, isolated spore with proximal suture split open. From hydrochloric acid maceration of coal ball 229 B 2 C.

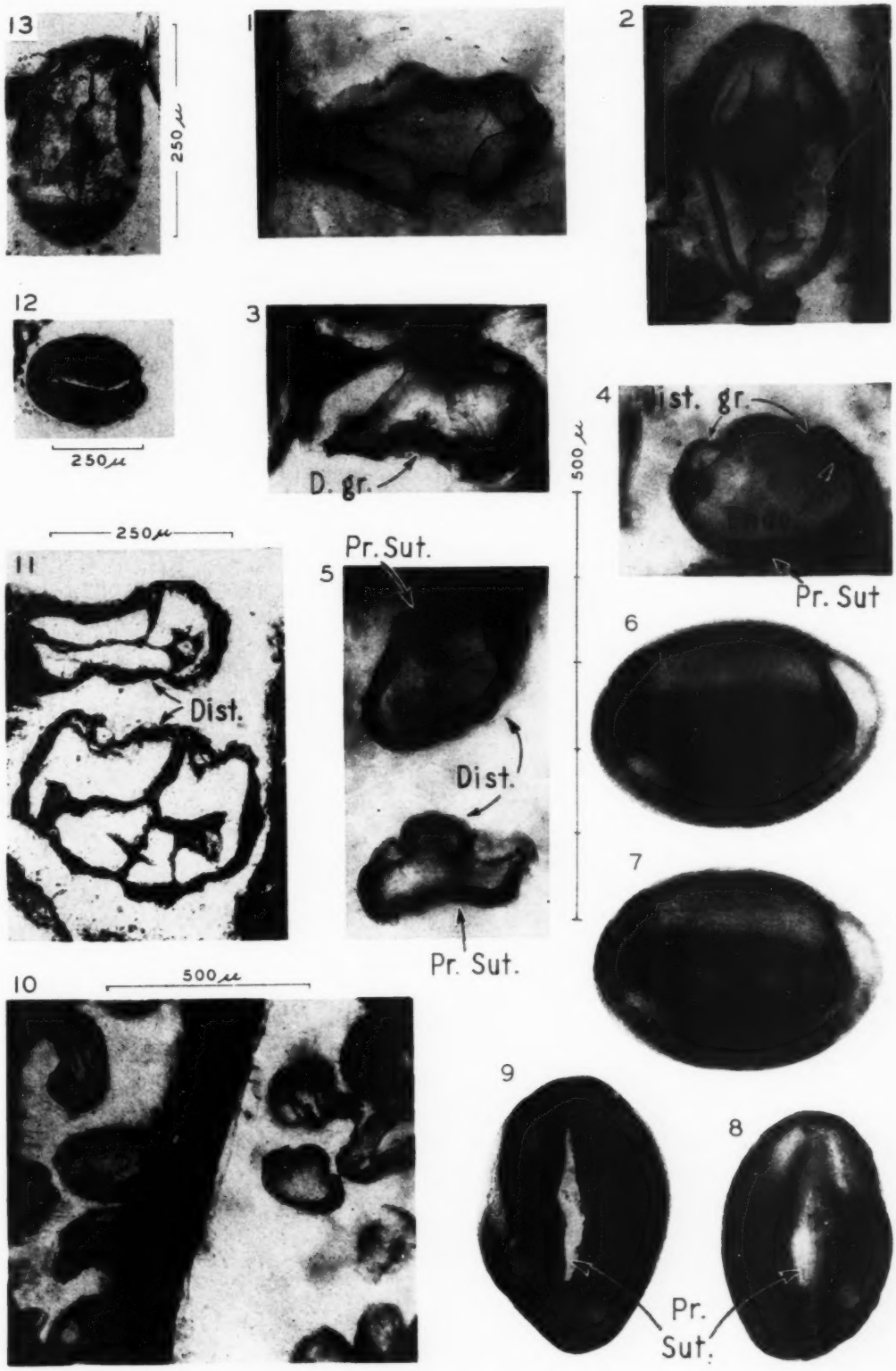
9—*D. formosa*, spore showing proximal suture open as in fig. *8*. Shadow outlines of distal grooves may also be noted in both figures. From hydrochloric acid maceration of coal ball 229 B 2 C.

10—*D. formosa*, spores in two adjacent sporangia. From coal ball 129 C (S 7).

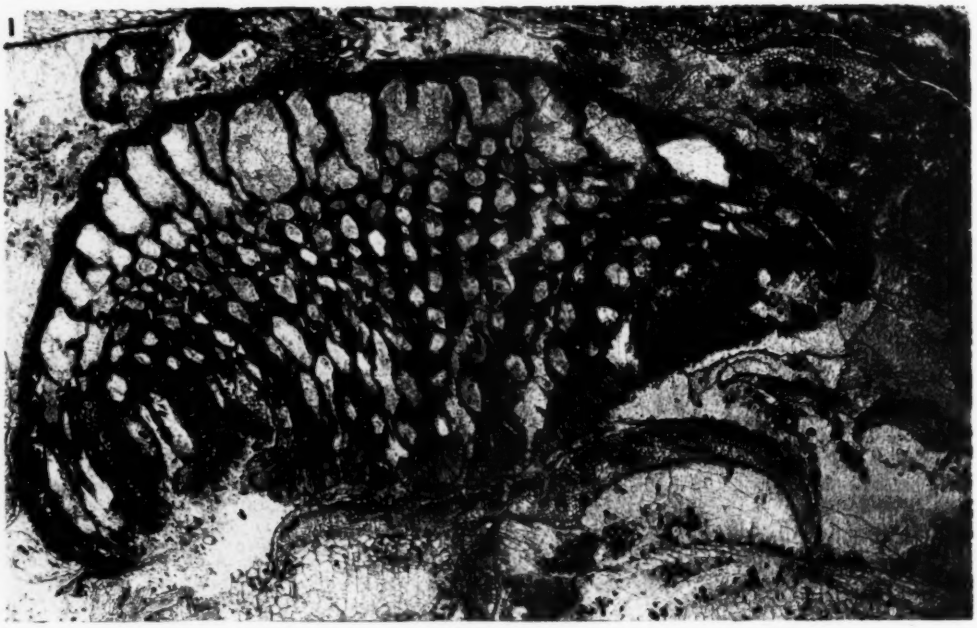
11—*D. fertilis* (Renault) Halle, sections of two spores probably showing endosporal gametophytic tissue. Details of the spore coat obscure. From Renault (fig. *4*, Pl. XII, 1902).

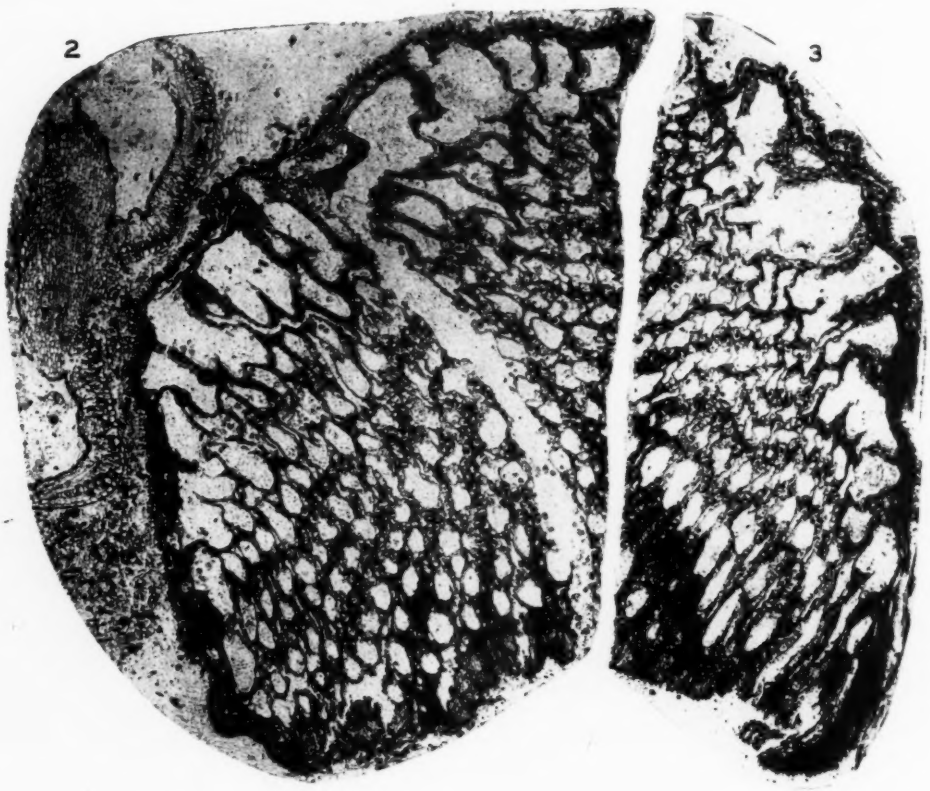
12—*D. fertilis* (Renault) Halle, spore showing proximal suture—evidently not one of the distal grooves. From Renault (fig. *3*, Pl. XII, 1902).

13—"*Aetheotesta* pollen," showing endosporal gametophyte possibly different from spore (prepollen) of *Dolerotheca*. From Renault (fig. *4*, Pl. XI, 1902).



Schopf, *Dolerotheca* spores





Schopf, *Dolerotheca villosa* n. sp.

(1902) cited the illustration copied here in plate 108 fig. 12, as proof of the opening of the distal umbo as an "operculum." It seems quite clear that this figure illustrates the proximal and not the distal side, and that the slit has occurred normally by way of the proximal suture as in spores of *D. formosa* discussed previously and shown in pl. 108 figs. 8 and 9.

The writer is inclined to attach considerable significance to the angular deflection of the proximal sutute. The sutures of monolete fern spores, e.g. those included in *Laevigato-sporites* (see Schopf, Wilson and Bentall, 1944, pp. 36–37) are not deflected in this manner. The tetrads have not been observed in *Dolerotheca* but the author entertains the possibility they may have shown tetrahedral arrangement and been relatively small. The *Dolerotheca* spores may have enlarged greatly after the tetrad separated and the deflection angle of the suture line may mark the trilete apex and point of departure of the third suture ray that has become obsolete.

The exosporal layer of the prepollen coat varies in thickness from about 8 μ in the trough of the distal grooves, to about 12 μ on the proximal side (cf. text fig. 13, and pl. 108, fig. 4. The exosporal coat also appears thinner at the two ends of the prepollen grains.

The endosporal membrane is generally present maintaining close contact with the proximal part of the exospore but more or less shrunken away from the distal side and ends. It is out of contact with the exosporal ridges on either side of the distal grooves in pl. 108, figs. 4 and 5 and can be observed shrunken from the exospore at both ends in the isolated grain illustrated in fig. 6. The evident folds in the endosporal membrane shown in fig. 6 are in no way due to compression.

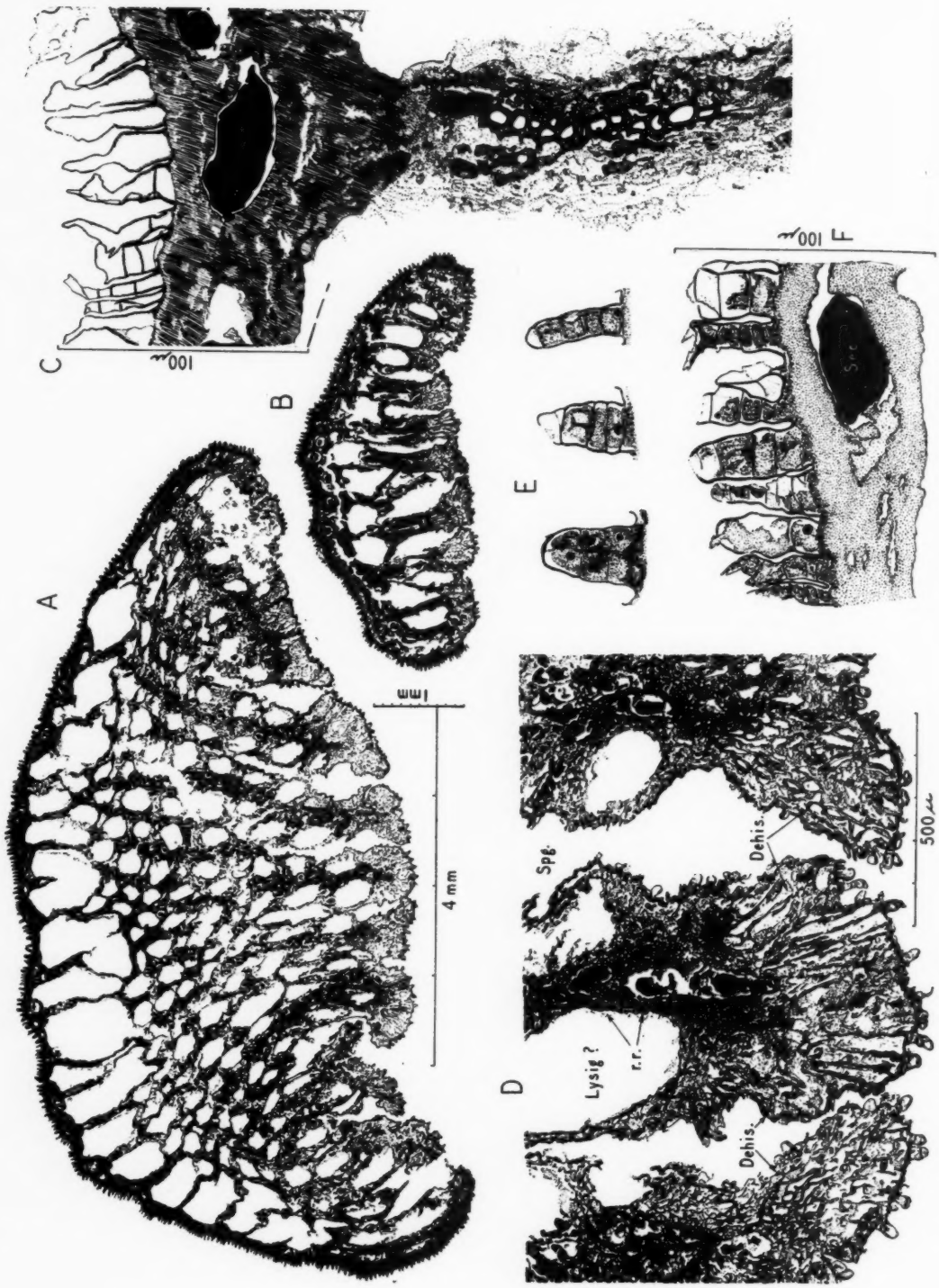
Observations by Renault (1902) and by Florin (1937) have shown beyond doubt that endosporal gametophytes are present in some types of well preserved Paleozoic spores, prepollen and pollen grains. The folded endosporal membrane within some grains of *D. formosa* was at first taken as a remnant of gametophytic tissue, but it seems now that this probably is not the case. Only in the sectioned example shown in text fig. 13 a, is there some question concerning the endosporal interpretation. Instances where the endosporal membrane is folded to simulate gametophytic tissue are shown in pl. 108, figs. 1–3, and may be compared with figs. 11 and 13 of the same plate (which have been copied from Renault) that probably do represent gametophytes. One could be more confident of Renault's interpretation if it were possible to distinguish both layers of the coat (exo- and endospore) as well as vesicular (gametophytic) contents.

Around the spore shown in pl. 108, fig. 1, is a calcite pseudomorph (indicated by the dashed line) which no doubt represents the former outline of the exospore before it partially collapsed during mineralization. Possibly the endosporal membrane also collapsed to its present invaginate outline at the same time. Identification of both layers is certain because the shrunken outer wall shown here resembles the exospore in color and texture and the thin invaginate inner structure is similar to more normally placed endosporal membranes. Plate 108, figure 3, shows an example in which the exospore is somewhat less shrunken, and the collapsed endospore less irregular than in fig. 1. In the lower central part of the figure is a small opaque cross, probably of pyrite crystals. Figure 2 of the same plate shows a spore in which the exospore is unshrunken but the endospore is severely collapsed. In all three instances it is the lack of any other membrane which could represent the endospore that renders a "gametophytic" interpreta-

EXPLANATION OF PLATE 109

FIG. *1*—*Dolerotheca villosa*, oblique longitudinal section through fructification; compare with text fig. 12a drawn from an adjacent peel section. The tip of an *Alethopteris* pinnule is associated below it. From coal ball 229 B 1a (t 10).

2, 3—*D. villosa* ,oblique peel sections taken adjacent to one another around 45° corner of fructifition. Associated *Alethopteris* pinnule in upper left. The presence of paired sporangial rows and intercalation of new rows is most evident in lower left of fig. *2*. From coal ball 229 B 2 A (s & b 2), magnification as for fig. *1*.


A
4 mm
1mm
B
C
100μ
D
Lysig ?
r.r.
Dehis.
Spb.
Dehis.
500μ
E
F
100μ
Src

tion most questionable. Possibly in fossilized material the walls of gametophytic cells might appear as if fused with the endosporal membrane. But if the membranes interpreted here as endosporal are in reality gametophytic walls, the cellular arrangement of the gametophyte must have been very irregular, to say the least, and the writer can see little definite evidence to support such an interpretation. Probably the gametophyte is the most delicate and least preserved "spore" part. If this tissue is present in any instance, the more resistant spore coat layers should also be accounted for.

Type Material.—The paratypes of *D. formosa* are these illustrated in pl. 104, figs. 1–7 etc. from coal balls 219 and 129 of the Illinois State Geological Survey collection. Should selection of a holotype specimen in any event be required, the writer would prefer to designate the one illustrated in pl. 104, figs. 1 and 2 from coal ball 219. The specimens are from the coal bed just below the Calhoun limestone near the town of Calhoun in Richland County, Illinois. This zone is in the upper part of the McLeansboro group of Illinois.[6]

DOLEROTHECA VILLOSA Schopf, n. sp.
Frontispiece, fig. C; Plate 109, figs. 1–3
Plate 110, figures 1–9, text figures 14, a–b

External Characters.—Male fructification about ¼ as large in external dimensions as *D. formosa* and more strongly convex proximally. Proximal surface slightly ridged radially; covered with close set villous hairs. Hairs adorn the lower distal surfaces of dehiscence tissue and are relatively longer and more numerous than in *D. formosa*.

A reconstruction drawn to the same scale as that of *D. formosa* is shown in the frontispiece, fig. C.

General Anatomy.—The tissues are essentially the same as in *D. formosa*. The sporangia are from 300–400 μ in diameter and perhaps as much as 5 or 6 mm. long, or about half as large as in *D. formosa*. Lysigenous cavities also occur as in the other species but they are proportionately smaller and less distinctly preserved. The general relations can be followed in the thin section shown in pl. 109, fig. 1, and text fig. 14 a, as drawn from an adjacent peel section. Plate 109, figure 2 shows peels taken from adjacent surfaces cut at right angles to one another. In pl. 110, fig. 1, and text fig. 14 b, are sections cut progressively more tangentially: The last is far enough out so that, for the short length represented, sporangial locules are cut in fairly good longitudinal alignment. The campanulary cover averages 200–300 μ in thickness and contains large secretory passages. Just below the integument is a row of large pores which seem to have arisen by lysigenous break-down of sporangial septae and other tissues. Each of the persistent septations between these enlarged pores contains an elongate series of tracheids cut transversely. The dehiscence tissue is present in very much the same relationship as in *D. formosa*.

The species is represented by two specimens in the material studied. These are somewhat complementary and afford an adequate basis for diagnosis but nevertheless are less well preserved than those of *D. formosa*. On account of the smaller dimen-

[6] Age relations of Illinois coal ball horizons are given in a previous publication (Schopf, 1941).

FIG. *14*—A. *Dolerotheca villosa*, oblique median longitudinal section of fructification from coal ball 229 B 1a.

B. *D. villosa*, nearly longitudinal section of same fructification near margin. Magnification, same for A and B.

C. *D. villosa*, section of campanulary cover with hairs, secretory cavity and septum containing vascular strand. From coal ball 229 B 1 a (t 8).

D. *D. villosa*, detail drawing of distal margin of longitudinal section showing epidermal hairs, dehiscence tissue (Dehis.), sporangia (Spg.), Lysigenous tube ? (Lysig.?) and resin rodlets (r.r.), in tissue above. From coal ball 229 B 1 a (t 8).

E. *D. villosa*, hairs from campanulary cover.

F. *D. villosa*, campanulary cover with secretory cavity (Sec.) and hairs with contents. Magnification same for E and F.

sions of *D. villosa* and its rarity it has not been possible to obtain as perfectly oriented sections as in *D. formosa*. Both specimens were cut obliquely. One is complete except that all spores have been shed. The other consists only of the central sporangial tissue and entirely lacks the campanulary cover layer, although the dehiscence layer is well shown. Some of the sporangia in the incomplete example contain a number of flattened and perhaps abortive spores. It seems likely that the cover from this specimen has broken loose from the included sporangia by the disintegration of septae which occur in partial dissolution in the other example.

The only tissues in either specimen which are in fair preservation are the hairs, the dehiscence tissue and the vascular strands. Parenchyma of the cover layer and intersporangial tissue have collapsed into a dark disorganized humic mass preserving only the external outlines and the contents of secretory cavities. The tracheid rows are clear enough but all the adjoining tissues are also reduced to a humic residue without visible cellular organization. It is difficult to account for the fair preservation of original form under these circumstances but there is little or no evidence of distortion.

Histology.—The hairs of the dorsal surface are 4–6 cells long, generally simple but occasionally biseriate. None of them appears to be capitate as are some of those present on *D. formosa;* they are much more closely spaced and differently shaped. The cells are filled with dark material and oftentimes a globular central body is present in each cell. The hairs are set very close to one another forming a villous felt on the proximal surface as much as 60–70 μ deep near the top of the fructification but becoming thinner toward the margin of the campanulum. Individual hairs are shown in text fig. 14 e. Their close arrangement is shown in text fig. 14 c and f; also in pl. 110, fig. 4.

The cover layer has many large secretory ducts with characteristic dark contents, 20–50 μ in diameter. They generally occur in a single series as shown in text fig. 14 c (sec.) and in pl. 110, fig. 4. No vascular strands or stone cells are discernible within the cover layer although this may be due to poor preservation. However it seems likely that the cover actually is less complex than in *D. formosa*.

Vascular strands seem to be limited to the persistent septae between the large pores located just below the dorsal cover. One of these septae is shown in its relation to the integument in text fig. 14 c. The section here, as in most of the others, is cut obliquely through the hemispheric fructification and is approximately at right angles to the surface of the campanulary cover at this point, which is about the highest in the section. Consequently the tracheid strands which run parallel to the outer surface are cut transversely. About 20 tracheids are shown in this group. Marginal walls of tracheids have broken down also so that probably there were a few more elements in the group originally. Smaller tracheids are seen at several places. Longitudinal sections as shown in pl. 110, figs. 7 and 8, show scalariform elements with the suggestion of an incipient bordered pit here and there in larger cells. The vascular strands seem somewhat more developed and the tracheids somewhat larger in *F. villosa* than in *D. formosa* where only small strands of characteristic spiral and annular tracheids have been observed.

The association of vascular strands with the mid-line of paired sporangial rows is somewhat more evident in *D. villosa* than in *D. formosa*, perhaps due to the collapse of all but the tracheid-bearing septae at the edge of the fructifications. Allowing for bifurcation of vascular strands wherever new sporangial rows are being intercalated toward the margin, it is apparent that the vascularized septae occur regularly along the midline of double series of sporangia, essentially similar to the apparent vascularization of *D. formosa*.

The breakdown of septae just below the cover has not progressed so far in the marginal region but none of the septae near the margin of the fructification contains tracheid strands. Apparently the tracheid bundles radiate only part way down the sides of the fructification. It seems that the vascular strands served for support well as as conduction in this type of fructification, but that the margins were sufficiently rigid that they required no special stiffening. The distance for translocation of materials was not very

great in this smaller fructification and did not require a more extensive vascular supply.

There is no evidence of sclerotic tissue in the fructification of *D. villosa*, although the preservation is not sufficiently good to prove that none existed. Since the hairs and dehiscence tissue, of thin walled cells which are not decay resistant are, nevertheless, well preserved, there is fair presumptive evidence that thicker walled sclerotic tissue was at least not well developed and may have been absent. The preservation does not permit a definite statement.

The intersporangial tissue shows little histologic detail. Large secretory ducts occur here, as in the cover layer, and penetrate down to the dehiscence tissue on the distal side (cf. text fig. 14 d and pl. 110, fig. 5, sec.). There also is a large number of smaller cells with similar contents scattered throughout. It seems that cellular structure was not preserved except where less perishable contents were present to mark more or less accurately the outline of original cell forms.

Dehiscence tissue is in general disposed as in *D. formosa* but it does not extend as deeply along the dehiscence grooves. Since the intersporangial ground tissue is not histologically interpretable, the relation of the dehiscence tissue to internal sclerenchyma strands cannot be made out. There is no evidence of this sclerenchyma, however, and it probably was rudimentary or absent.

Although sometimes obscure, an epidermal layer can be identified covering the distal surfaces as in *D. formosa*. This emphasizes the probability that no prismatic specialization of the epidermis occurs on sporangia of this group of plants. The hairs on the distal epidermis also are more numerous than in *D. formosa*. They are 2 or 3 cells (50–65 μ) long, as shown in text fig. 14 d and in pl. 110, figs. 6 and 9. The terminal cell of each hair is rather abruptly triangular.

Spores or Prepollen.—The specimen constituting the basis for most of the foregoing description has matured and shed all its spores. They are present however in the second more fragmentary specimen, previously mentioned. Prepollen spores are 130 to 150 μ long and 100 to 120 μ broad, with typical proximal sutures and two distal grooves as in *D. formosa*. The spores have collapsed for the most part and no accurate thickness measurement is possible, but the spore coats seem normally thick, and if they are abortive, this occurred in the last stages of growth. The example shown in pl. 110, fig. 2, is from a peel and the distal side has been partially torn away revealing the well defined suture on the proximal side. In figure 3 of pl. 110 a group of more or less collapsed spores is shown inside a sporangial locule. The distal grooves of the large spore at the left are barely distinguishable in the photograph but may be observed in the section at higher magnification by placing it over a concentrated point of light. Thus in structure these spores are typical of *Dolerotheca* but they are the smallest for any species yet reported.

Type Material.—Both specimens used in this description are from the same locality as those of *D. formosa* previously described. There is no question that distinct species are represented for not only do they differ in size and proportions at maturity, but the pubescence and other features are distinctive. The specimen which should be considered as the holotype is from coal ball 229 of the Illinois State Geological Survey collections. The more fragmentary specimen with collapsed prepollen grains is from coal ball 215.

DOLEROTHECA REEDANA Schopf, n. sp.
Plate 111, figures 3, 4; plate 112, figures 2–6; plate 113, figures 1–6; plate 114, figures 1–9, 14, 15; plate 115, figure 9; text figure 15

External Characters.—Male fructification campanulate, slightly more inflated proximally than *D. formosa*. Diameter estimated at 15–20 mm.; central thickness about 7½ mm. Proximal (dorsal) side glandularly pubescent, irregular, covered with verrucosities of varying size and prominence, upon which hairs are particularly numerous. Radial indentions of the integument, if present, are rendered obscure by the surface irregularities. The distal surface is slightly convex, with dehiscence grooves ½ to 1 mm. deep. As in the other species, a definite epidermal layer covers the distal

surface, the cells of which serve as bases for hairs or papillae. Distal hairs lack the dark contents characteristic of those of the proximal cover and are slightly more slender with terminal cells more cone-shaped.

General Anatomy.—The holotype specimen of *D. reedana* is located on the edge of a coal ball so that somewhat less than half of it is preserved; nevertheless enough is present to afford a fairly accurate and complete description. The largest available section is that shown in pl. 111, fig. 4. As shown in that figure the lower central part (lower left) is missing or poorly preserved. The central part of the dorsal cover proper has been destroyed, possibly by intrusion of roots. A much flattened *Psaronius* (?) root is shown at the top of the figure on the left where at least the outer part of the campanulary cover is mising. The unusually thick parenchyma shown just below this foreign root can be followed by a somewhat tenuous but undeniable connection with the more characteristic fructification structure toward the right. The largest vascular strands yet observed in *Dolerotheca* appear in this parenchymal region and one of them is illustrated in pl. 111, fig. 3. Probably the peduncle attachment was close to this point. The presumed peduncle (described later) is not attached but probably belongs to this specimen with which it is closely associated. It is located above the better preserved part of the cover and to the right of the root as shown in pl. 111, fig. 4. It is also illustrated in pl. 112, figs. 2 and 6. The tissues below the peduncle (?) are rather well preserved and one sporangium is cut longitudinally from top to bottom. The more marginal sporangia are also poorly preserved but may be observed in other sections (pl. 112, figs. 2 and 6). The margin of the campanulary cover is everywhere observable on the side of the specimen, notwithstanding spotty preservation of marginal sporangia.

There are two other *Dolerotheca* fragments in the same coal ball which appear to correspond with the type specimen. The fragments show some tissue structure, chiefly in the transverse plane, but the most valuable information they afford is in regard to the spores. Spores in the type specimen are all more or less collapsed.

In addition to the *Dolerotheca* fructification and fragments and the peduncle which probably goes with them, a fragmentary *Myeloxylon* petiole, in part well preserved, is also present in the same coal ball. The possible correlation of these on the basis of histologic structure is discussed later.

The sporangia of *D. reedana* occur in paired rows and presumably they radiate from the center of the fructification as in the other species. However, nearly all the sections available are longitudinal and the characteristics shown best by transverse sections cannot be as accurately established. The sporangia are 350–400μ in diameter and the longest sporangium seen is slightly more than 6 mm. in length; a few sporangia may be slightly longer. The longest sporangia seen are on one side of the center of the fructification and show a slight sigmoid curvature which is somewhat more pronounced in shorter sporangia near the margin.

The lysigenous tubes are clearly shown between sporangia of each radial series. They are relatively large, measuring about 400 by 100–200μ in diameter, with the shorter diameter crowded between the radially adjacent sporangia of the rows. The cells surrounding the tubes have considerably thicker walls than the ground tissue although their dimensions are similar. Possibly the breakdown of tissue inside the cavities has contributed to this appearance.

Dehiscence tissue and fibrous sclerenchyma are present and in general have the same relative position as these tissues in *D. formosa*. Spores were shed through slit-like perforations in the dehiscence tissue as in the other species. No specialized mechanism to produce dehiscence has been noted. Vascular strands are located on the middle radius of paired sporangial rows and alternate with the rows having sclerenchyma strands. In *D. reedana* the vascular strands are more prominent throughout their length, than in the other *Dolerotheca* species. Possibly a combination of fortuitous factors is more responsible than any great biological difference. The radial sections of *D. reedana* are favorable for their observation, and the tracheids of the bundles are larger than in *D. formosa*. Three of the vascular bundles are

cut transversely in some of the sections in the area near the top of the fructification and they probably are only a very short distance from the point at which the peduncle was attached. These bundles are elongated in outline, 300–400μ long and 50–90μ broad (see text fig. 15). Small tracheid

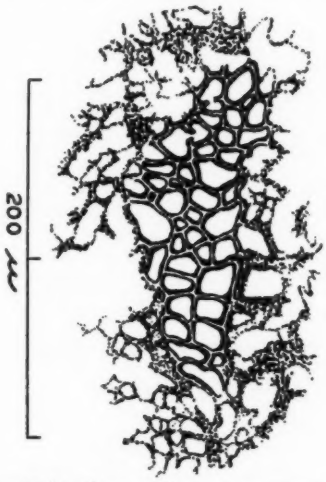


FIG. *15*—*Dolerotheca reedana*, transverse section of large vascular strand from campanulary cover close to the probable attachment of peduncle. From coal ball H b 208 B (b 1).

strands branch from the lower edge of the elongate bundles and penetrate downwards between the sporangia (see pl. 111, fig. 3, and pl. 112, fig. 5). The cover layer is vascularized nearly to its periphery by small remnants of the deeply situated plate-like strands.

Histology.—The hairs on the proximal cover are more numerous than in *D. formosa* but they are not as closely set as in *D. villosa*. They range from 40 to 80μ in length and consist of from 3 to 5 cells. Most hairs are peg-like with a round tapering tip but some are clavate or capitate tipped as shown in pl. 113, figs. 1–3. Clusters of hairs cap the warty protuberances of the surface; sometimes this gives the illusory appearance that the hairs branch at the base, as for example, those at the right of pl. 113, fig. 1. Dark shrunken remnants of the cell contents are nearly always evident and sometimes dark nucleus-like bodies are present like those shown in both cells of the short capitate hair in fig. 3.

The epidermis of the campanulary cover consists of small rather thick-walled, nearly isodiametric cells with dark contents (cf. pl. 113, fig. 3). Subdermal tissues also are secretory in appearance though also more definitely parenchymatous. A slightly denser zone of less well preserved cells appears at a variable depth below the dermal layer. In general this zone appears more regular in outline than the surface, due to the presence of the verrucose protuberances of the latter. In some respects the dark layer appears as if it were an incipient pellogen although no clearly distinguished secondary tissue has been produced.

Below the dark layer is a zone of spongy parenchyma. Intercellular spaces are evident as shown in pl. 113, figs. 1 and 2. Secretory cells and resin rodlets are interspersed in the spongy parenchyma as in *D. villosa* but they are less abundant. Sclerids, isolated or in groups, also occur in the spongy tissue. Vascular strands are located near the interior of the spongy zone as shown in pl. 113, figs. 1 and 2, and may mark the internal limit of the cover layer. The tissue internal to the bundle zone of the spongy parenchyma is of the characteristic type which also surrounds the sporangia, i.e., the ground tissue of the fructification. The cover layer thus defined has a thickness of $\frac{1}{2}$–1 mm. depending on whether the end of a sporangium is adjacent (causing it to be a little thinner) or whether measurement includes the thickness of one of the external verrucosities.

The intersporangial ground tissue in *D. reedana* is generally similar to that in *D. formosa*. Secretory cells and resin rodlets are present in the ground tissue as in the other species; they are less abundant in *D. reedana* than in *D. villosa* although individually the secretory cells and rodlets are slightly larger.

As in the other two species, the tissue directly surrounding sporangia is not well preserved. Plate 113, fig. 6, shows a segment of sporangium in longitudinal section with remnants of the original sporangial wall best shown on the left side. The dark membrane is composed of two layers and apparently represents the remains of cells whose end walls have disintegrated. Probably this also indicates the mode of origin of a sporangial

membrane such as described within sporangia of *D. formosa*.

The dehiscence layer is essentially similar to that of the other species. The cells appear shorter however with less oblique end walls. Plate 113, fig. 4, shows the appearance of this tissue; a large resin rodlet of the ground parenchyma appears at the upper left of the figure.

The distal epidermis also is clearly shown in pl. 113, fig. 4. Cell contents are present and the walls appear somewhat thickened although this may have been caused by mineralization. There is no distinction between "thickening" of periclinal and anticlinal walls of the epidermis, and no close comparison can be made with the prismatic layer of cryptogamic sporangia. Nearly every cell serves as a hair base or has a strong central papilla as shown in pl. 113, fig. 5, from a section parallel to the epidermis along a dehiscence groove. Only a few hairs are visible in fig. 4 taken at right angles to a similar surface.

The dehiscence tissue merges with strands of fibrous sclerenchyma as in *D. formosa*. Relative to the size of the fructification the sclerenchyma seems a little more developed in *D. reedana*, but in the absence of good transverse sections this is not certain.

The vascular tissues of *D. reedana* can be followed more adequately than in either of the other species despite the rather fragmentary condition of the available specimens. The fragments of tissue shown at the upper left in pl. 111, fig. 4, show vascular bundles 300–400μ long and 50–90μ broad which must not be far removed from the peduncle attachment. These are also illustrated in text fig. 15, pl. 111, fig. 3, pl. 112 figs. 3 and 5, and pl. 115 fig. 9. The elongate form of these bundles is most characteristic and similar to those of *D. villosa*. Small elements centrally located in the bundles may represent protoxylem. Preservation is not good enough to show definitely the location of phloem although possibly a few phloem elements were present on both sides. Small vascular strands which penetrate the radii between sporangia are evidently given off from the lower edge of the elongate bundles as shown in pl. 112, fig. 5. The main bundles of the cover layer continue nearly to the margin of the fructification although there they are considerably diminished in size. One of the larger bundles near the center of the fructification has been twisted before mineralization so that the pitting can be observed. Part of this bundle is shown at higher magnification in pl. 112, fig. 3, to illustrate the characteristic scalariform and reticulate thickenings. The tracheids are broader than those of *D. formosa* and commonly exceed 20μ in diameter. The vascular strands between sporangia are composed of tracheids of more uniform size than those in the cover itself, and possess similar pitting as shown in pl. 112, fig. 4.

Spores or Prepollen.—The holotype of *D. reedana* contains numerous spores of the prepollen type which are nearly all collapsed. It is evident that this is not the result of petrifaction but was induced earlier, possibly even before this particular fructification was

EXPLANATION OF PLATE 110

FIG. *1*—*Dolerotheca villosa*, oblique longitudinal section of fructification about half way from the center to the margin. From coal ball 229 B 1a (12), scale of magnification indicated below figure (12.5×).

2—*D. villosa*, spore (prepollen) from peel section showing the proximal suture. The distal side of the spore has torn away from the peel. From coal ball 215 C (B 1), (172×).

3—*D. villosa*, sporangial locule full of partially collapsed spores. From coal ball 215 C (B 1), (172×).

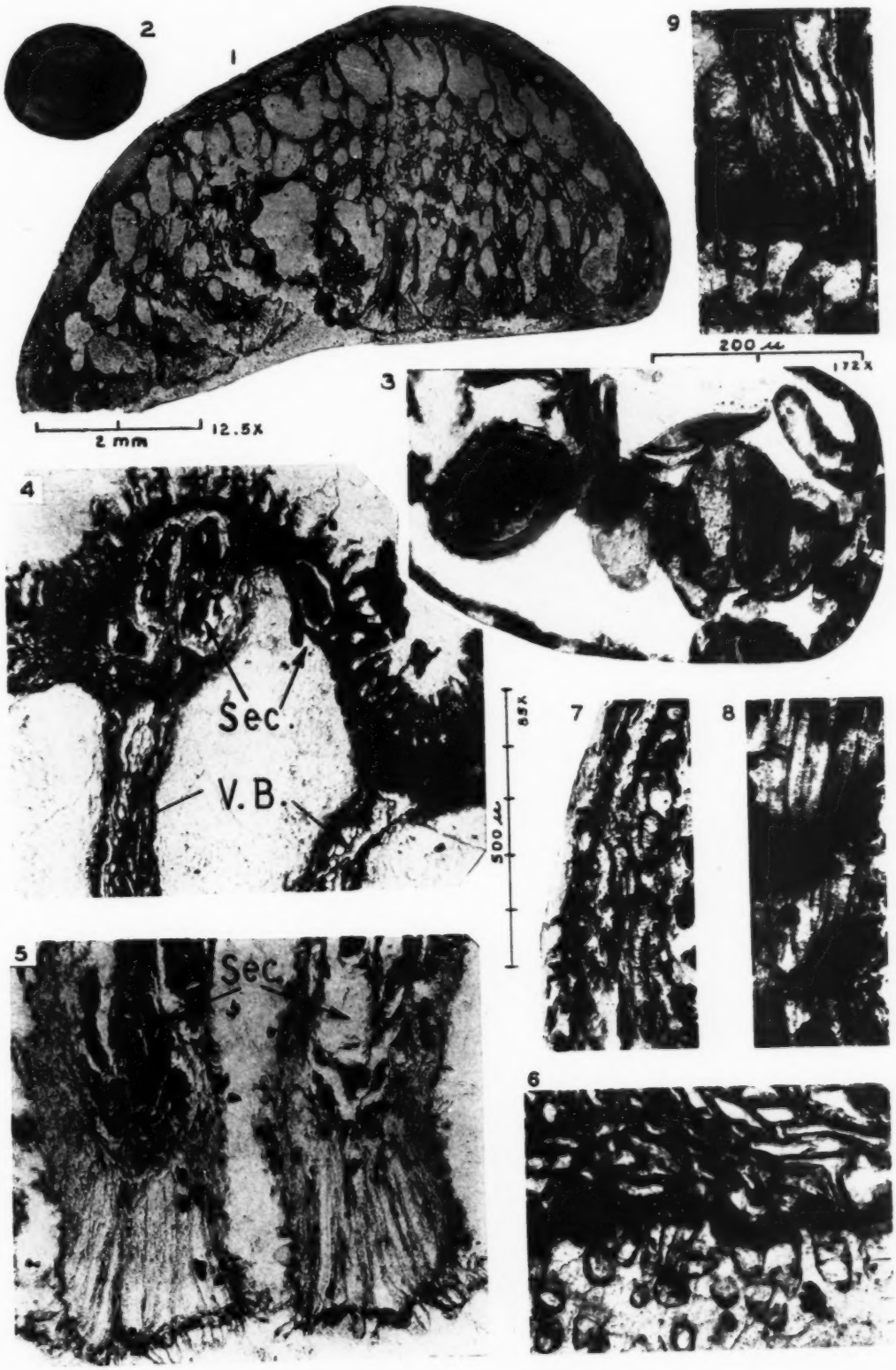
4—*D. villosa*, section of cover layer showing close-set hairs above, secretory chambers (Sec.), and persistent septae with vascular bundles (V.B.) cut transversely. From coal ball 299 B 1a (t 6), scale of magnification indicated at right (85×).

5—*D. villosa*, section of dehiscence tissue showing epidermal hairs, sporangial pores, and secretory canals (Sec.) in tissue above. From coal ball 229 B 1a (t 23), magnification same as fig. *4*.

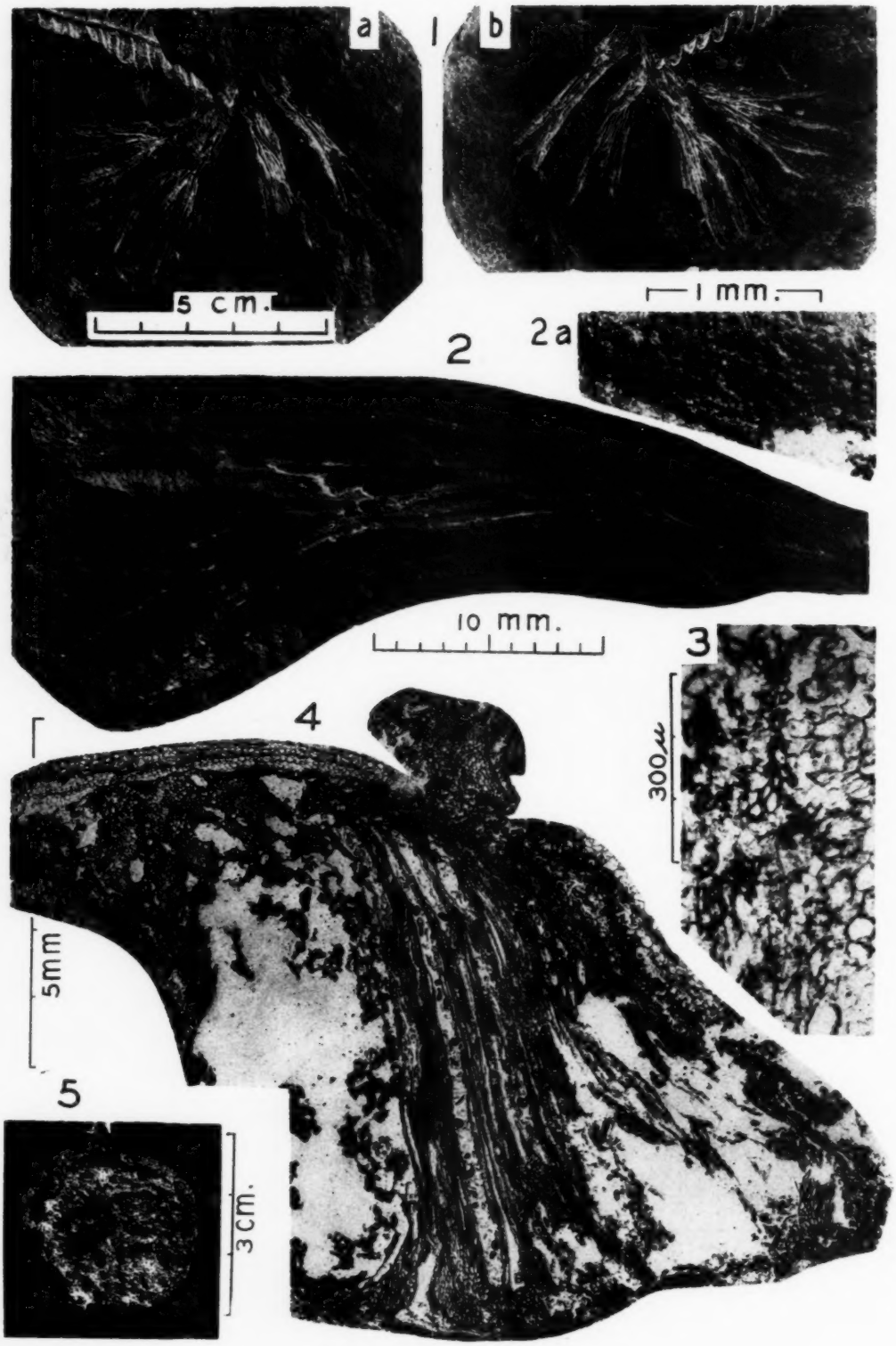
6—*D. villosa*, oblique section across edge of dehiscence tissue showing epidermal hairs. From coal ball 229 B1 a 1 (t 6), magnification same as fig. *3* (172×).

7, 8—*D. villosa*, longitudinal sections of vascular bundles showing irregular type of scalariform elements. From coal ball 229 B 2 a (S& B 2) & (S 5), magnification same as fig. *4* (85×).

9—*D. villosa*, edge of dehiscence tissue showing epidermal hairs. From coal ball 229 B 1 a 1 (t 6), magnification same as fig. *3* (172×).



Schopf, *Dolerotheca villosa* n. sp.



Schopf, *Dolerotheca, Codonotheca*

incorporated in the litter of the peat swamp. The two other *Dolerotheca* fragments present in the same coal ball contain normal spores which are numerous both within and outside of sporangia. The ordinary course of events may have involved general fragmentation of the fructification after the spores matured and fragmentary campanulas like these associated with the uncollapsed spores may be typical. The description of the spores has been drawn chiefly from those in the more fragmentary specimens and not from the collapsed spores in the holotype fructification shown in pl. 113, fig. 6. There can be little doubt that they are specifically identical because, aside from preservation, all the significant characters agree. Many of the normal and uncollapsed spores were isolated by breaking off a fragment containing a portion of a fructification and dissolving the calcite matrix in dilute hydrochloric acid, as was done in the case of *D. formosa*.

The spores of *D. reedana* are very similar to those of *D. formosa* and isolated specimens would be very difficult to distinguish in ordinary coal maceration residues. Individual isolated spores from both of these species would probably be classified as *Monoletes ovatus* (see Schopf, Wilson and Bentall, 1944, p. 38) if no other information was available. Slight differences in size and shape are detectable when spores are uncompressed as these are of *Dolerotheca*, but such slight differences probably cannot be relied upon to separate them if they have previously been compressed.

The prepollen spores of *D. reedana* range from 260 to 325μ long and from 165 to 250μ broad. Although in size they overlap the lower size range of *D. formosa* spores, in general they appear more broadly ovate. The proximal suture is distinct and generally marked by an angular deflection near the center as seen in pl. 114, figs. 1–4. This deflection of the proximal suture seems a trifle more pronounced than in *D. formosa*. The two distal grooves are very prominent but never appear to be split open by natural dehiscence. The spore coat is 5 to 6μ thick at the bottom of the grooves as shown in pl. 114, fig. 5 (Dist. gr.), and each groove is marked by a definite narrow furrow in the coat as shown in fig. 8 of the same plate. The thickness of the spore coat increases to 7 or 8μ outside the furrow near the axis of each groove and then thickens gradually to about 12μ on the distal umbo and to as much as 18μ on the thicker proximal region. The distinction between the proximal suture and distal grooves is evident by the fact that in cross section the suture shows a line of parting extending through the spore coat. The spore shown in median cross section in pl. 114, fig. 15, has split open along this proximal suture line.

Spore surfaces are ornamented only by very fine granulose punctation. In section the coats seem to show obscure radiating striation which may possibly be due to a type of micellar organization.

The endosporal membrane is well shown in many spores dissolved out of the calcite matrix wherever it shrunk away from the

---

EXPLANATION OF PLATE 111

FIG. *1a, b*—*Codonotheca caduca*, group of four fructifications attached to a common fertile branch. The two fructifications best shown appear naturally bilaterally symmetrical. Both halves of a specimen from Mazon area, Will and Grundy Counties, Northern Illinois (Carbondale formation, Shale above Illinois No. 2 coal); Ill. State Museum Catalog No. 14326. Slightly reduced.

2—*Codonotheca caduca*, fructification showing surface striation and pubescence (punctate surface due to hair bases). *2a*, Surface of specimen at greater magnification. Specimen from Mazon area, Ill. State Museum Catalog No. 3001.

3—*Dolerotheca reedana*, transverse section of elongate bundle near top of fructification, with smaller vascular strands diverging from it below. From coal ball Hb 208 B (b 4).

4—*D. reedana*, longitudinal section of fructification, with peduncle (?) above. Spores appear as dark spots or lines in the one sporangium cut in good longitudinal alignment. From coal ball Hb 208 B (b 4).

5—*Dolerotheca* sp. Compression from specimen, surface slightly concave. From a "Mazon type" nodule from Carterville, Williamson County, Southern Illinois, from basal McLeansboro shale above the Herrin (No. 6) coal. Ill. Geol. Surv. Catalog No. S B 79, nearly natural size.

outer wall (cf. pl. 114, fig. 5). It is distinctly seen in pl. 114, figs. 14 and 15, but appears to be discontinuous. This discontinuity is probably an artifact induced when the nitrocellulose peels were being prepared. The spores of *D. reedana* thus far have not shown any of the pseudo-cellular (?) endosporal configurations which are prominent in some of the spores of *D. formosa*. If this is at all significant it probably is due to slight differences in the manner of mineralization.

Type Material.—The holotype of *D. reedana* is from Harrisburg (HB) coal ball No. 208, collected for the Illinois State Geological Survey by A. C. Noé, from Harrisburg (No. 5) coal, O'Gara No. 9 mine (open pit), located near the southeast corner of section 21, T. 9 S., R. 6 E., just south of the city of Harrisburg, in Saline County, Illinois. This coal bed lies stratigraphically somewhat above the middle of the Carbondale group of Illinois.

NOTES ON RELATED FOSSILS

The same coal ball in which *D. reedana* was discovered contains a *Myeloxylon* petiole and a small poorly preserved structure which probably is the peduncle of the *Dolerotheca* fructification. This presumed peduncle is described first and evidence bearing on its possible correlation with the species of *Myeloxylon* follows. An impression specimen of *Dolerotheca* preserved in an ironstone concretion is described and discussed and some recent observations on the Whittleseyinean genus *Codonotheca* are presented.

DOLEROTHECA REEDANA peduncle (?)
Plate 111, figure 4; plate 112, figures 1, 2, 6; plate 115, figures 6–8; text figure 16

This is a small (about 2 mm. in diameter) originally triangular (?) structure which extends about 5 or 6 mm. along the top of the *D. reedana* holotype. It is badly fragmented for most of its length so that it cannot be described very satisfactorily. Although it occurs in the closest possible association with this *Dolerotheca* specimen, there is no actual proof of its immediate connection. Its suggested function as the peduncle of *Dolerotheca* is chiefly based on the structure of epidermal hairs which are well preserved, in part, and correspond closely with those of the dorsal cover of the *Dolerotheca* fructification.

The close association of this peduncular structure is shown in pl. 111, fig. 4 and pl. 112, figs. 2 and 6. A line diagram of the peduncle, text fig. 16, shows its epidermal hairs

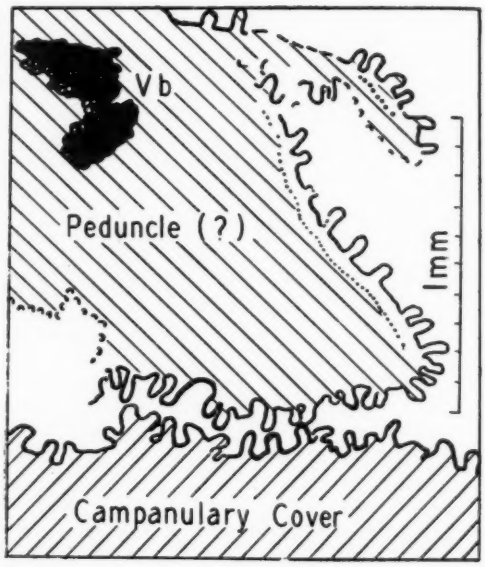


FIG. *16*—Sector of *Dolerotheca reedana* campanulum and probable peduncle, showing the intimacy of association in coal ball H b 208 B. Photo tracing from section (b 6).

to be nearly interlocking with those of the campanulary cover of the fructification below, and their similarity is obvious. Another more fragmented portion which shows the hairs well is illustrated in pl. 112, fig. 1, and at higher magnification in pl. 115, fig. 6. The description of hairs of the dorsal cover layer of *D. reedana* applies equally well to these. The only difference noted is in their arrangement on the epidermis. The hairs of the peduncle are not situated on tubercular outgrowths as they commonly are on the fructification. Some are very close together but in general they are fewer and less closely spaced.

The epidermis of the peduncle is quite distinct and shows no evidence of any irregular cell divisions. The epidermal cells contain

dark contents but are not obscure on this account, as are many of the dorsal epidermal cells of the campanulas. There is no indication of any sclerotic tissues in the peduncle. The ground tissue is parenchymatous and includes a few resin rodlets as shown in pl. 112, fig. 1 (R) and pl. 115, fig. 6.

It has not been possible to ascertain the nature of the entire vascular complement of this specimen because at least half of it is poorly preserved throughout its length. The vascular bundles differ considerably in form from those in the proximal part of the *Dolerotheca* fructification as may be seen by comparing fig. 8 (peduncle) and fig. 9 (fructification) shown at the same magnification on plate 115. There is considerable similarity in size of the elements of both and in the pitting. Vascular bundles of both are chiefly composed of scalariform tracheids. The peduncle bundles seem probably mesarc and may be concentric, but phloem is too obscure to be confidently identified. The outline of the most evident bundles is shown in text fig. 16 (V.B.). Perhaps the chief vascular bundle in pl. 115, fig. 8, and other figures may be in process of dichotomizing, but if so, the fission requires a distance of several millimeters for completion. The pattern of vascularization of the petiole is not clear because two or possibly three other bundles which belonged to it are disconnected and variously distorted. One of these appears at the lower left in pl. 115, fig. 8. Because of this distortion it is not certain that this peduncle was essentially radial in its symmetry rather than dorso-ventral.

The close agreement between epidermal hairs of *D. reedana* and this peduncle, the great similarity of elements of the vascular bundles and the conjunction of other factors, although individually merely suggestive, when taken together furnish rather convincing indication that the peduncle pertains to that species.

MYELOXYLON, cf. M. AMERICANUM (Hoskins)[7]
Plate 115, figures 1–5

A segment of a petiole probably referable to *Myeloxylon americanum* is present in the same coal ball that contains the holotype of *D. reedana*. Its identification with Hoskins' species is not immediately evident by comparison with figures published with the original description. However, comparison with the original slides showed that *M. americanum* is more variable than suggested by Hoskins and that the specimen under consideration agrees with it in many features. Some of Hoskins' slides show a heavy zone of radially elongated subdermal sclerenchyma extending nearly continuously around the margin on one side. In other places, these sclerenchyma strands are tangentially elongated and less prominent. Adjacent to the thick marginal sclerenchyma, the sclerotic "caps" accompanying vascular bundles and secretory canals are very heavy, but they become progressively thinner toward the center of the petiole where there is almost no sclerotic bundle sheath. Sclerotic caps of moderate development are irregular in marginal outline as seen in transverse section. Resin rodlets are fairly numerous and possess no distinct epithelial layer of cells. Cells of varying size, averaging slightly smaller than those of the ground parenchyma, enclose the secretory ducts. Thin tangentially elongated epithelial cells such as those present in the Nashville myeloxyla associated with *Medullosa distelica* (cf. Schopf, 1939) do not occur. Petiolar secretory canals in Nashville specimens are all about the same diameter. In *Myeloxylon americanum* there is a wide variation in the size of the canals, many of them are large and contain typical resin rodlets but others are much smaller and some are similar in size to large parenchyma cells of the ground tissue. In fact, numerous evenly distributed parenchyma cells also appear to have secretory contents. The gradation seems to be complete between ducts of the two extremes in size.

The *Myeloxylon* fragment in the *Dolerotheca* nodule from Harrisburg does not have the extremely heavy sclerenchyma present

[7] Originally described as *Angiospermophyton americanum* (Bot. Gaz. vol. 75, p. 390, 1923), this species is referable to *Myeloxylon*. The author has personally consulted the types which are part of the collection of the Illinois Geological Survey, and verified the opinion originally expressed by Seward (1923). The species seems to be well represented in the Harrisburg coal balls.

in parts of the type specimen of *M. americanum*. It appears to agree in most particulars with less sclerotic portions of that species, however, and probably cannot be distinguished from it.

One small area of the specimen associated with *D. reedana* seems to lack subdermal sclerotic tissues entirely, even in the proximity of marginal secretory canals. A portion of this area is shown in pl. 115, fig. 1. The marginal vascular bundles all possess a definite sclerotic bundle sheath, however, and the one shown in pl. 115, fig. 2, is typical. The phloem of this bundle (Ph) is excellently preserved and unusual in this respect. Generally phloem tissue is lacking as in the bundle shown in plate 115, fig. 3. The presence of a secretory duct adjacent to the xylem and enclosed by the sclerotic bundle sheath in fig. 3 is exceptional. Protoxylem as identified by small tracheids is chiefly concentrated next to the phloem as in the type of *M. americanum*. Some small tracheids also occur which are not in proximity of the phloem but it is questionable whether these are actually protoxylem elements. They may be merely small cells of the metaxylem which were late in development and failed to enlarge fully. It is also possible that they represent only the tapering ends of normal metaxylem elements. The large metaxylem elements shown in pl. 115, fig. 3, are gathered in two groups, possibly preparatory to bifurcation.

A large characteristic secretory canal and resin rodlet with sclerotic tissues somewhat separated is shown in pl. 115, fig. 4. Two smaller canals with less sclerotic development but situated in about the same relative position in the petiole are shown in fig. 5.

BIOLOGIC CORRELATION OF THE PEDUNCLE(?) OF DOLEROTHECA REEDANA AND MYELOXYLON AMERICANUM

The evidence for concluding that the hirsute peduncle described above belongs to *D. reedana* has been presented. It is desirable also to consider further the histologic evidence which supports the correlation of this structure with *Myeloxylon*, since some such relationship may fairly be presumed to have existed.

Although it seems probable that *Medullosa*, *Myeloxylon*, *Dolerotheca* and others are correlative genera in Pennsylvanian strata (and possibly through most of this system) there is as yet no evidence to show how, i.e., on what particular part of the plants, the male fructifications were borne. They may have been attached to the ultimate rachides of an *Alethopteris* type frond. Some evidence now indicates that seeds were borne in this manner (Halle, 1927, Arnold, 1937). It is equally plausible that the male fructifications may have been borne on special fertile branches somewhat as suggested by the specimen of *Codonotheca* illustrated by Darrah (1938) and by the specimen shown in Pl. 111, fig. 1 (no. 14326 of the Langford collection in the Illinois State Museum, Springfield). A similar fruiting habit has recently been described for *Lacoea seriata* by Read (1946) and a comparable occurrence is shown by *Goldenbergia glomerata* (Halle 1933). It is also conceivable that the male fructification was attached directly to the main axis, arising in the axil of a leaf base near the tip of the stem, or, if the fruit bud was dormant for a time, its position might have been farther down the trunk. Un-

---

EXPLANATION OF PLATE 112

FIG. *1*—Peduncle (?) probably of *Dolerotheca reedana*, showing resin rodlet (R) and epidermal hairs. From coal ball Hb A (t 4).

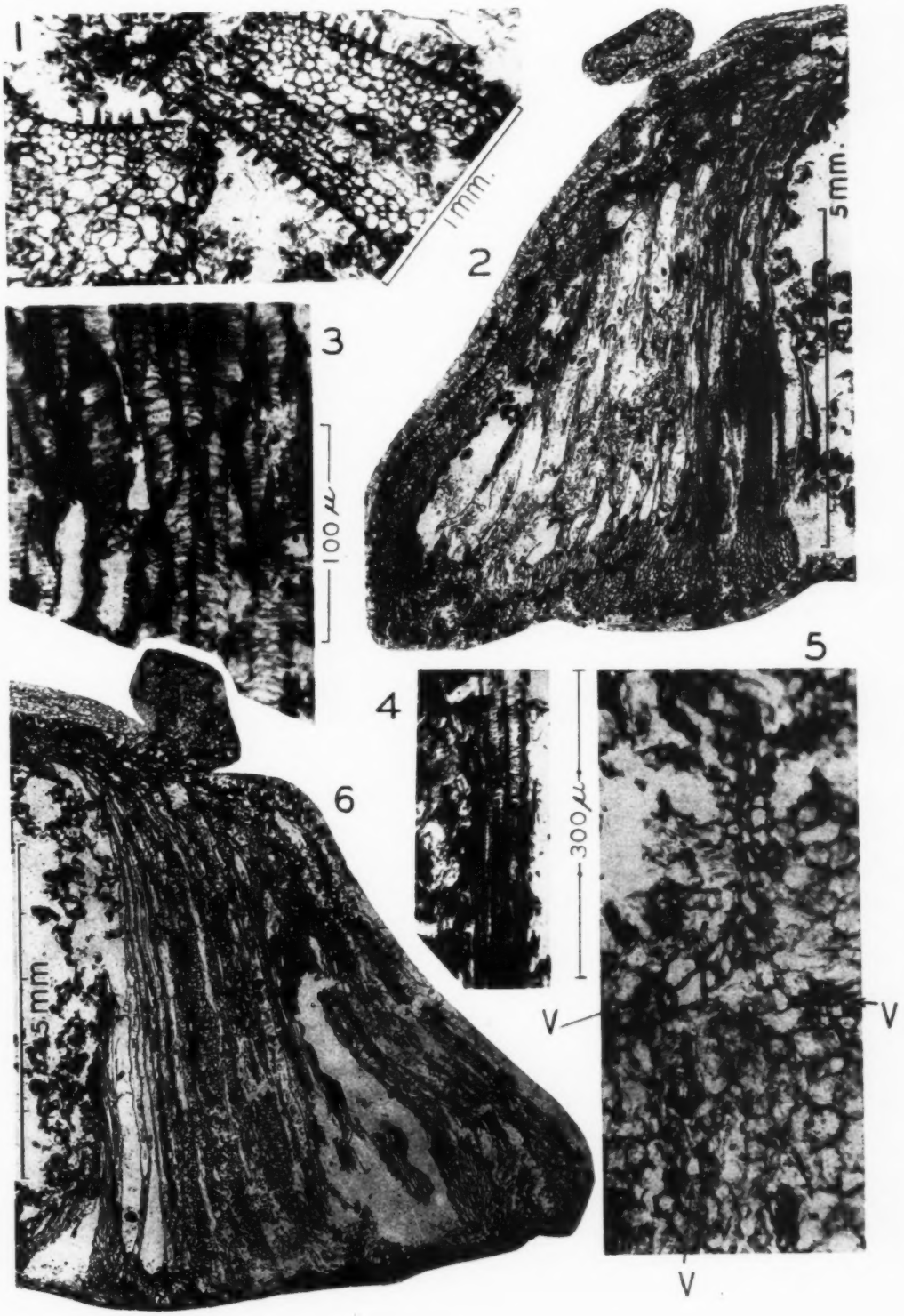
2—*Dolerotheca reedana*, longitudinal section at margin of fructification with peduncle (?) above. Distal (dehiscence) surface is irregular because the section is obliquely transverse to the dehiscence grooves. From coal ball Hb 208 B (t 3).

3—*D. reedana*, longitudinal section of vascular bundle near top of fructification showing irregularly reticulated and scalariform elements. From coal ball Hb 208 B (B 4).

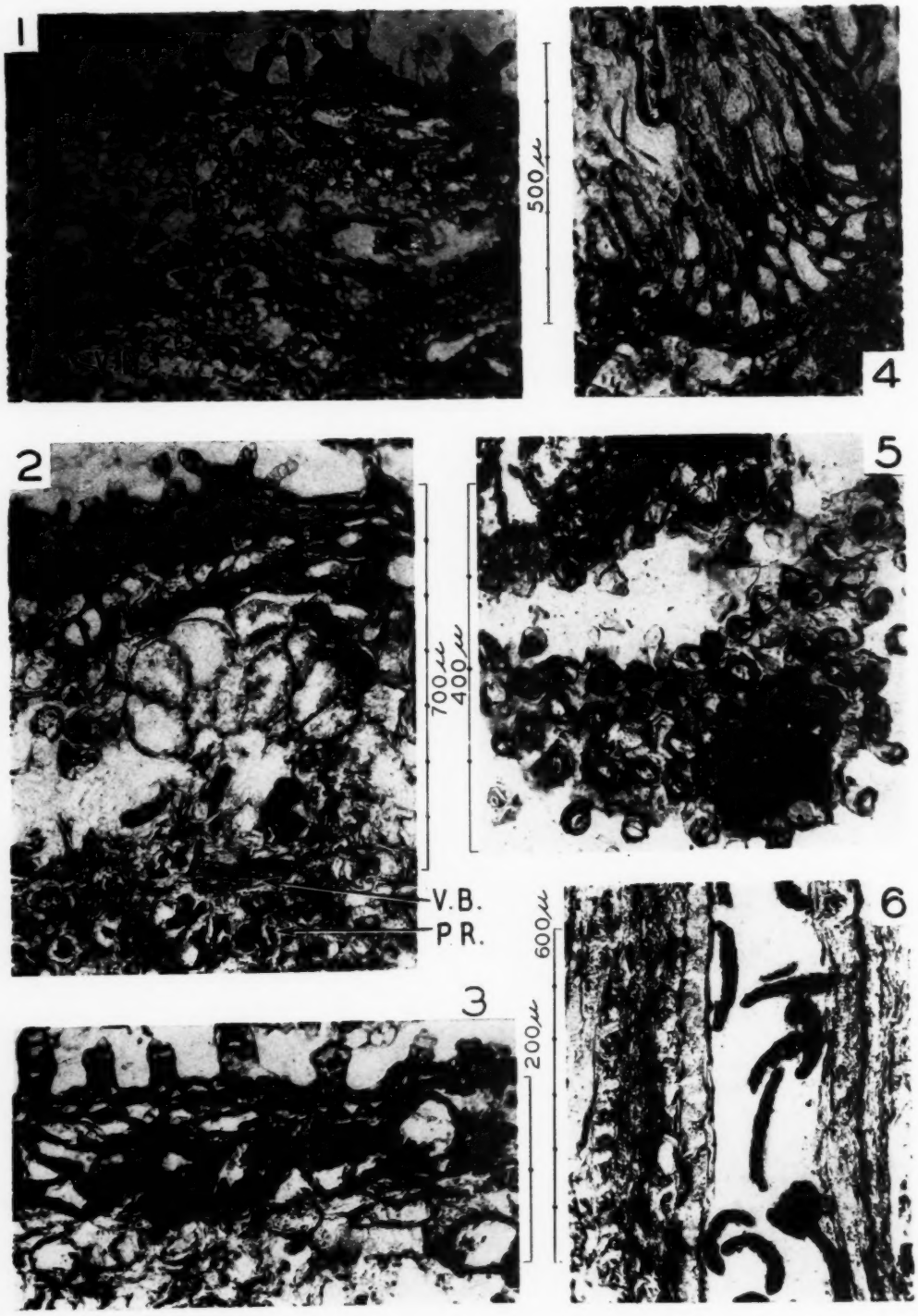
4—*D. reedana*, longitudinal section of vascular strand near margin of fructification. From coal ball Hb 208 B (b 2).

5—*D. reedana*, transverse section of vascular bundle near top of fructification showing small strands (v) given off below. From coal ball Hb 208 (b 2), magnification same as fig. 4.

6—*D. reedana*, longitudinal section at margin of fructification with peduncle above. From coal ball Hb 208 B (b 10).



Schopf, *Dolerotheca reedana* n.sp.



Schopf, *Dolerotheca reedana* n.sp

fortunately there is no evidence directly bearing on the condition in *Dolerotheca*.

The extent of agreement or disagreement between structures of the *Dolerotheca* peduncle and large *Myeloxylon* petioles possibly should not be emphasized. There is no known reason to assume that these structures should be very similar, even if they were parts of the same plant. They are functionally diverse organs of long standing no matter what the structural similarities or dissimilarities may be.

Plate 115, figures 1–7, shows portions of the *D. reedana* peduncle (figs. 6–7) and of *Myeloxylon* cf. *M. americanum* (figs. 1–5) at the same magnification for comparison. *M. americanum* has no epidermal hairs so far as known although associated and probably correlated pinnules of *Alethopteris* are hirsute on the lower surface and some hairs are also present on minor divisions of the rachis. The foliar hairs are more slender and less glandular than these of the peduncle and present no particularly convincing points of similarity although all of them appear to be uniseriate.

Aside from the absence of hairs the *Myeloxylon* epidermis agrees fairly well with that of the peduncle. The epidermal cells of the petiole are darker due to greater deposits of secretory (?) material than in the peduncle, as may be seen by comparing figs. 1 and 6 of Pl. 115. The petiole also has a distinct cuticle which is separated slightly from epidermal cells in the portion shown in fig. 1. These epidermal differences might be disregarded as due to differences in ontogenetic age. The peduncle probably grew quickly and persisted only a short time whereas it seems likely that the large petioles were at least as permanent on these plants as the petioles are in living cycads.

Plate 115, figure 1 shows an area where the subdermal sclerenchyma is essentially absent. This condition is probably not unusual in *Myeloxylon*. It seems clear that the development of sclerenchyma is variable to a considerable extent and that much of the variation has not yet been systematically described. The normal variation due to relative position in the petiole, i.e., whether ultimate, penultimate, or main divisions of the rachis, has not been accurately ascertained for most species and until this is done specific identifications of *Myeloxylon* specimens will be of doubtful value except where precise homologies can be established for comparison. Thus it is not entirely clear what emphasis should be placed on the very subordinate development of sclerenchyma in the small section represented in fig. 1 except that it is rather comparable in appearance to the subdermal tissue of the *Dolerotheca* peduncle.

Although the vascular strands of the fructification and peduncle of *Dolerotheca* offer some strong points for comparison, neither shows much similarity to the collateral bundles of the *Myeloxylon*. The peduncle vascular strand shows no clear distinction between protoxylem and metaxylem as in the petiolar bundles and there are considerable differences in the size of elements (compare fig. 7 with figs. 2 and 3 of pl. 115 which are reproduced at the same magnification). The largest cells of the

---

EXPLANATION OF PLATE 113

FIG. *1*—*Dolerotheca reedana*, section of cover layer showing hairs mounted on small verrucose protuberances. Note position of vascular bundle (V. B.). From coal ball Hb 208 B (b 4).

2—*D. reedana*, section similar to fig. *1* but somewhat better preserved. Note the numerous secretory cells (R. R.) below and in the vicinity of the vascular bundle (V. B.). From coal ball Hb 208 A (t 4).

3—*D. reedana*, section of outer part of cover layer showing hairs, one of which is capitate, epidermis and dark incipient phellogen (?) layer below. From coal ball Hb 208 B (t 3).

4—*D. reedana*, section of lobe of dehiscence tissue showing epidermis and hairs, secretory canals in tissue above. From coal ball Hb 208 b (B 18), magnification same as fig. *1*.

5—*D. reedana*, section in part parallel to lobe of dehiscence tissue showing number and arrangement of epidermal hairs. From coal ball Hb 208 C′ (t 2).

6—*D. reedana*, section of a sporangium containing collapsed spores. The row of cells bounding the sporangial locule on the left is more delicate than the rest of the intersporangial tissue and may indicate the nature of the sporangial membrane seen in *D. formosa*. From coal ball Hb 208 B (B 18).

peduncle bundles are about the size of protoxylem elements in the *Myeloxylon*. Whether small ultimate divisions of the rachis would show more similarity to the peduncle in vascularization cannot be stated now although it is known that the vascular elements are smaller in the ultimate petiolar branches.

The peduncle of *Dolerotheca* is similar to the *Myeloxylon* petiole in that both possess similar secretory canals. In fig. 6, a resin rodlet is situated in the ground parenchyma similar to the one shown in fig. 1. Although they are fewer in the peduncle both have very similar ground parenchyma.

Such similarities probably are insufficient evidence for biologic correlation, but the differences also are inconclusive because dissimilar organs are being compared. A more pertinent comparison might be possible between ultimate divisions of the *Myeloxylon* rachis and the peduncle.

Dolerotheca impression

An interesting specimen of *Dolerotheca* was collected by the writer in 1938 from near Carterville, Williamson County, Illinois. It was found upon splitting one of the ironstone concretions of the Mazon Creek type which occur there in grey shale overlying the Herrin (No. 6) coal. This coal bed is accepted arbitrarily as the top member of the Carbondale formation, hence the fossil is from the lowermost McLeansboro. Although plant preservation is similar, this zone is considerably younger than the classical one at Mazon Creek. Anatomical features being absent, it seems inadvisable now to apply a specific designation to this specimen although it probably is distinct from the other species. The chief point worthy of note is the generic identification of the form, a point which seems reasonably established in spite of the differences in preservation existing between this and the other *Dolerotheca* specimens. This occurrence gives some basis for hope that the geologic record of *Dolerotheca* and allied genera will be further augmented by compression and impression specimens. Coal ball petrifactions can be counted on to provide a basis for anatomical interpretation but such specimens are relatively scarce and, therefore, usually do not constitute a main source for information desired in stratigraphic problems. This additional specimen of *Dolerotheca* suggests that the genus may not be as rare in the Pennsylvanian beds of America as the scant literature indicates.

Description of the three American species of *Dolerotheca* has shown that the vascular strands are located rather deeply within the dorsal cover layer. This may well afford a good basis for distinguishing *Dolerotheca* from seemingly perfoliate cyclopterid leaf impressions which may superficially correspond in outline. The cyclopterids show venation clearly whereas it may be doubted that *Dolerotheca* ever does (also see Florin, 1926). An obscure radial alignment of sporangial impressions appears to be most characteristic of impressions and compression specimens of *Dolerotheca* (cf. Halle, 1933, pl. 9, figs. 5 and 6).

Dolerotheca sp.

Plate 111, figure 5; plate 114, figure 10

Fructification nearly circular in outline, about 28 mm. in diameter; the campanulary cover is indicated by the rim 2–3 mm. wide around the margin. Sporangial rows are shown by more or less definite protuberances radiating from center. Prepollen grains are large, about 450μ in their longest dimension and about 390μ in the shortest; proximal suture and distal grooves of the prepollen are evident; the prepollen coat is finely granulose. Anatomical details unknown.

The specimen has suffered considerable compression and most of its original carbonaceous content is gone. The cavity formerly occupied by compressed tissues has been partly replaced by a friable film of calcite and kaolinite in which some carbonaceous fragments still are present (pl. 111, fig. 5). A few prepollen grains are present in this friable semi-mineralized layer and may be observed under a Greenough-type microscope. They show no definite arrangement to indicate the form of sporangia and it is evident that they had mostly been shed before fossilization. One of the spores remaining is shown in pl. 114, fig. 10. Twenty or more spores, all of the same kind, have been observed and this seems sufficient evidence to indicate that these examples are not foreign to the specimen.

The characteristic spores and the nearly

circular form of the fructification with no indication of lobes or appendages make the generic identification of this fossil certain. It may, however, be distinct from other species because its spores are somewhat larger and more broadly oval. In size the fructification is intermediate between *D. reedana* and *D. formosa*. With the exception of its larger spores, this form seems intermediate between these well characterized species.

Other compression specimens which may be congeneric are those described as *Daubreeia* (in part) (White, 1903, p. 107; Sellards, 1908, pp. 430–433),[8] *Doleropteris pennsylvanicum* (Dawson 1890, p. 7), and possibly, judging from White's (1903, p. 107) discussion, also the *Plinthiotheca angularis* of Lesquereux. It should be stressed that the presence of prepollen or other proof of sporogenous nature is of critical importance in identifying any of these with *Dolerotheca*. Thus far this has not been shown, but it may be if reinvestigation is undertaken using modern improved methods. However, the specimen illustrated as *Daubreeia* (?) by Sellards (1908) in pl. 56, fig. 5 of Vol. 9 of the Kansas Survey is particularly suggestive of *Dolerotheca*. It is about 21½ by 25 mm. in diameter and seems to show radiating sporangial rows with additional rows intercalated toward the margin. It was collected from the LeRoy shale near Blue Mound in Kansas.

CODONOTHECA

Codonotheca is one of the genera included by Halle in the Whittleseyineae. It has been definitely identified chiefly in nodules from the Mazon Creek area in Grundy and Will Counties of Northern Illinois. Some observations have been made on a few specimens which are of interest in the present connection.

CODONOTHECA CADUCA Sellards
Plate 111, figures 1, 2; plate 114, figures 11-13

The specimens are all much flattened. In part this may be attributed to pressure resulting from burial but the author believes that a good deal of the asymmetry in cross section is original, since the Mazon nodules often preserve surficial form without much distortion. According to this interpretation the *Codonotheca* fructification consists of a single loosely paired row of tubular sporangia. Free ends of the sporangia penetrate the matrix so that it is difficult to accurately ascertain the number but it seems there were commonly six and may sometimes have been eight in all. Sellards (1903) and subsequent authors have all considered the *Codonotheca* fructification to be radially symmetrical. If *Codonotheca* and other Whittleseyineans were bilaterally instead of radially symmetrical and composed essentially of a single double series of tubular sporangia, they would seem to show greater correspondence with the structure of *Dolerotheca*.

The author is not yet prepared to accept fully Halle's conclusion as to the uniseriate whorled arrangement of sporangia and the hollow interior of the Whittleseyinean forms. The lamina-like form of *Whittleseya* was accepted without controversy by students of fossil plants for many years and further evidence is needed before the view long held is completely discarded. A bilateral interpretation of *Codonotheca* at any rate, would seem equally acceptable.

A further character of *Codonotheca* which seems to have escaped particular notice is the pubescence of the outer surfaces. Sellards (1903) mentioned longitudinal striae and weaker cross lines which no doubt represent the impressions of epidermal cells and in the description of his fig. 15, pl. 8, he stated that fig. 17 shows the "minutely roughened or pitted surface". The pits mentioned are acutally hair bases which appear to be more or less glandular and closely set. In distribution at least, they are similar to those of *Goldenbergia* and *Dolerotheca*. It is not unusual for the ironstone matrix of Mazon concretions to preserve such surface features faithfully and the specimen shown at slight enlargement in Pl. 111, fig. 2 shows the "punctate" surface characteristically. In fig. 2a of this plate, a densely pitted surface of the same specimen is shown at greater magnification. The bases of hairs can be seen penetrating the matrix surrounding *Codonotheca* but the shape of

[8] Specimens of *Daubreeia* in the U. S. National Museum, including three of those studied and illustrated by Sellards, show clearly that they are not fertile organs comparable to the *Dolerotheca* campanulas. They appear, at least superficially, more like *Dolerophyllum* (see Florin, 1925).

the hair itself is not commonly exhibited. In a few instances they appear relatively long and tapering; more so than the hairs of *Goldenbergia* shown by Halle (1933, pl. 2, figs. 18-19). The *Codonotheca* surfaces are best observed by reflected illumination with the Greenough type microscope when the specimens are flooded with xylol. The author regards the occurrence of these hairs as further confirmation of Halle's assignment of *Codonotheca* to the Whittleseyineae, and as additional evidence linking the Dolerothecan and Whittleseyinean subtribes.

The recognition of a definite pubescence on *Codonotheca* is useful and aids in the identification of fragmentary or otherwise questionable specimens. For example, examination of the originals of illustrations labeled *Codonotheca cadua* in pl. 43, figs. 1 and 2, of Bull. 52 of the Illinois Survey are shown by this criterion to be wrongly identified. The original of fig. 1 is more likely a tuft of lycopod leaves similar to the *Lepidodendron rigens* of Lesquereux. That shown in fig. 2 is probably a whorl of inflate *Annularia* leaves which were originally deposited somewhat distorted from their usual position. On the other hand the specimen in fig. 3 of the same plate shows the characteristic pubescence near the basal part and is no doubt correctly identified even though no spores are visible in the three sporangia exposed. Erroneous identification of specimens as *Codonotheca* is by no means rare in collections from the Mazon beds of northern Illinois.

Spores or Prepollen.—The folds shown on spores of *Codonotheca caduca* by Darrah, and thought by him to be similar to the distal grooves and umbo of other Dolerosporeae, were considered by Florin (1937) to be a "single long and broad germinal furrow." According to the present author's interpretation this "germinal furrow" is only a chance structure caused by incidental collapse or folding. Only one spore out of the fifteen or more illustrated by Darrah shows folds definitely enough to support the possibility of distal specialization. Since this one spore appears to be unique even in the original figures, the writer is inclined to question whether it has any special significance. Spores of *Codonotheca* are illustrated in pl. 114, figs. 11-13 and these show nothing that can be interpreted either as distal

---

EXPLANATION OF PLATE 114

Magnification same for figs. *1–13*, scale indicated.

FIG. *1*—*Dolerotheca reedana*, spore (prepollen) showing strongly bent proximal suture. Spore isolated from fructification by solution of calcite matrix in hydrochloric acid. From coal ball Hb 208.

2—*D. reedana*, isolated spore showing proximal suture. From coal ball Hb 208.

3—*D. reedana*, isolated spore showing very moderate deflexion of proximal suture. From coal ball Hb 208.

4—*D. reedana*, isolated spore similar to fig. *2*, proximal suture appears under different illumination due to the presence of a bubble of CO_2 inside the spore coat.

5—*D. reedana*, isolated spore showing endosporal membrane in plane of focus. From coal ball Hb 208.

6, *7*—*D. reedana*, spores showing umbo and distal grooves. From coal ball Hb 208.

8—*D. reedana*, spore tilted to one side showing thin area at bottom of one of the distal grooves. From coal ball Hb 208.

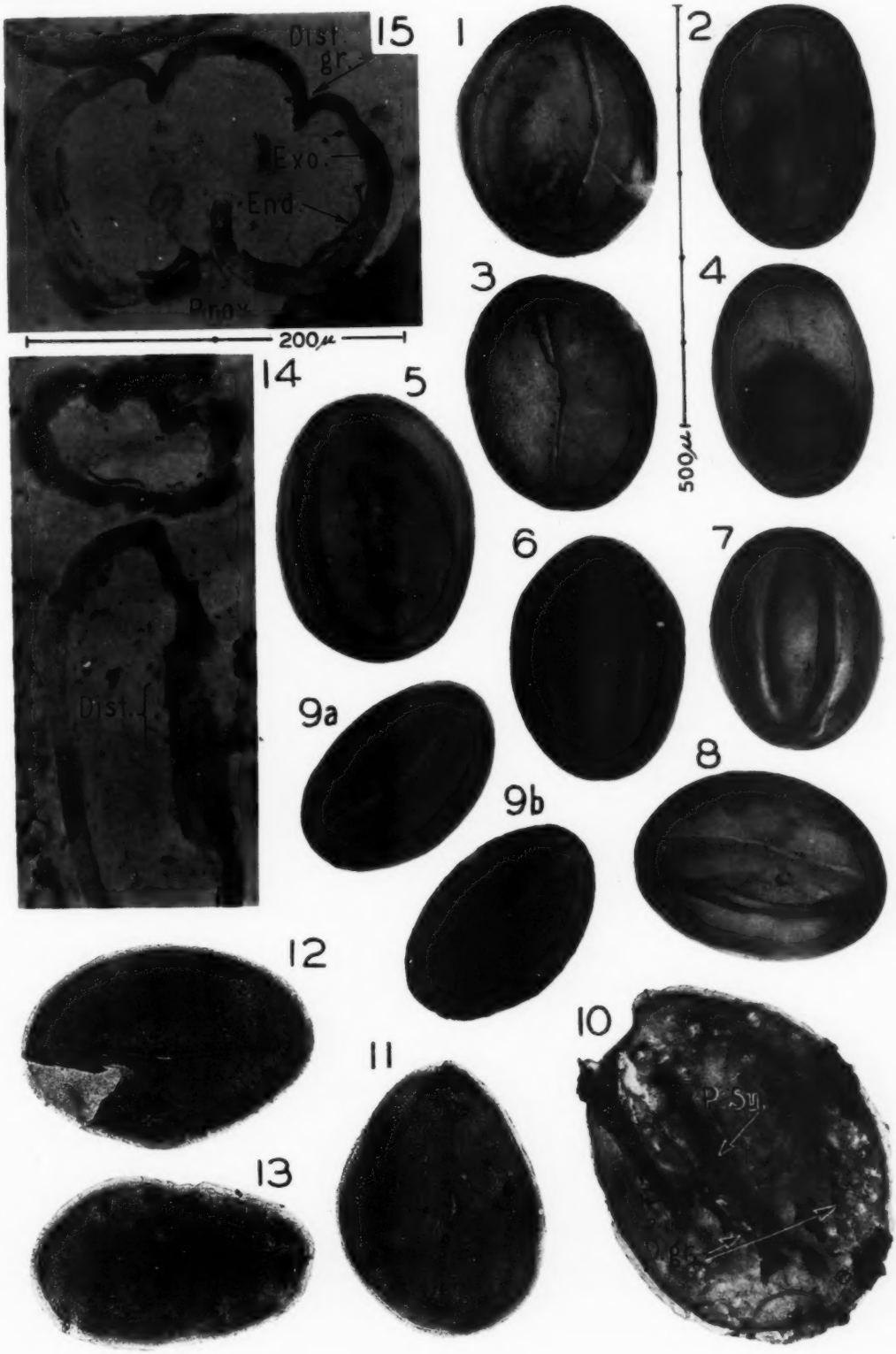
9—*D. reedana*, spore photographed to show proximal suture (*9a*) and at a lower plane of focus to show distal grooves (*9b*). From coal ball Hb 208.

10—*Dolerotheca* sp., large spore from compression specimen shown in Pl. 111 fig. *5*. P.S.—Proximal suture, D. gr.—distal grooves. Ill. Geol. Survey Catalog No. S B 79.

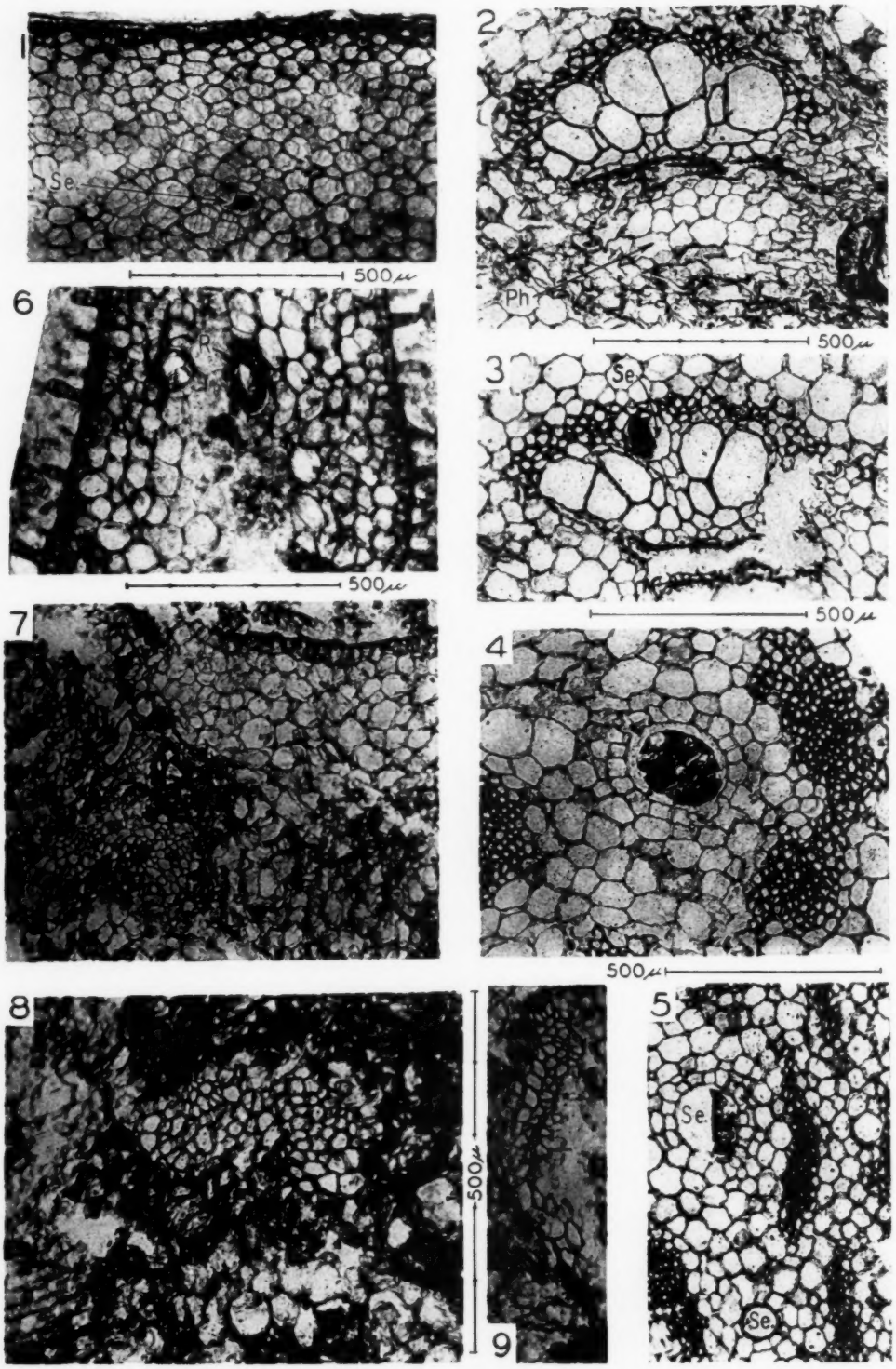
11–13—*Codonotheca caduca*, spores showing proximal suture only. Photographed at the same magnification and other conditions as those shown in figs. *1–10*. From specimen from Mazon area, Ill. Geol. Surv. Catalog No. S B 1006.

14—*Dolerotheca reedana*, peel section including (above) the tip of one spore cut transversely, distal side up, and spore sectioned longitudinally (below), one of the distal grooves (Dist.) cut obliquely at the right. From coal ball Hb 208 D (B 1), magnification indicated above figure.

15—*D. reedana*, median transverse section of spore showing distal umbo and grooves above and spore coat split open below along the proximal suture. Dist. gr.—distal groove; Exo—exospore layer; End—endosporal membrane; Prox.—proximal side. From coal ball Hb 208 D (B 1), magnification same as fig. *14*.



Schopf, *Dolerotheca, Codonotheca* spores



Schopf, *Myeloxylon americanum* and *Dolerotheca peduncle* (?)

grooves or a "germinal furrow." In these spores the proximal suture and granulose surface texture are the only distinctive features. Their shape and size correspond with other members of this pteridosperm alliance. It is true that incidental folds sometimes are present, but, according to the writer's interpretation, *Codonotheca* spores lack any discernible vestige of distal apparatus. If specimens occur which have distal specialization they probably should not be identified with Sellards' *Codonotheca caduca* because his description obviously is accurate for those of the Mazon specimens this writer has examined. The similarity of material examined in connection with the present study to Sellards' original description shows that *C. caduca* is an accurately defined species.

PHYLOGENETIC CONNECTIONS

Up to the present time *Dolerotheca* has occupied a somewhat isolated systematic position because it was not known in sufficient detail to permit accurate comparison. It is hoped this deficiency has been largely overcome by the material that has been described above. In the paragraphs below the writer suggests a relationship for *Dolerotheca* with other pteridosperms. Unless one adopts the view that the seed habit associated with pteridosperms arose spontaneously in several independent phyletic lines, and therefore that the group as known today is a highly polyphyletic and unnatural one, some hypothesis of mutual relationship is called for, even though it may be held tentatively and by no means regarded as proved in detail.

The writer believes there is ample evidence to indicate the lygenopterid and meddullosan pteridosperms are monophyletically related, that is, derived ancestrally from a single common stock, and the following discussion is based on this assumption. These two groups include the pteridosperms best known and they constitute the nuclear material of reference for the pteridosperm group as a whole in the consideration of all modern authors.

Since 1930, Zimmerman's telomic concept of organization of higher plants has been used comparatively because of its simplicity, and because of its recognition of fertile organs as fundamental units in the make-up of plants, a view that has long been advocated by F. O. Bower and others concerned with fundamental interpretation of botany. Complex fructifications may arise by the aggregation of fertile telomic units so that the result is a synangium in the strict sense. Probably they also may arise by enlargement and elaboration of a single fertile telome. The structure of the *Dolerotheca* campanulum seems to be more readily explained by the latter evolutionary process, and the sort of elaboration it prominently displays is regarded by the writer as most easily explained by a process of septation.

Any elaborated fructification of this type

EXPLANATION OF PLATE 115

Magnification same for figs. *1–7*, scales indicated.

FIG. *1*—*Myeloxylon* cf. *M. americanum*, non-sclerotic margin of petiole. Note cuticle and secretory duct (Se). From coal ball Hb 208 B (B 18).

2—*M.* cf. *M. americanum*, vascular bundle with sclerenchyma sheath moderately developed. Note phloem (Ph.) which is well preserved. From coal ball Hb 208 C (t 2).

3—Bundle similar to that in fig. *2* but lacking the preservation of phloem—a secretory duct (Se) is located next to the xylem within the sclerotic sheath.

4—*M.* cf. *M. americanum*, resin rodlet and sclerenchyma strands moderately developed. From coal ball Hb 208 C (t 2).

5—*M.* cf. *M. americanum*, area near margin of petiole showing a moderate development of sclerenchyma strands and small secretory canals (Se). From coal ball Hb 208 C (t 2)

6—Peduncle (?) probably of *Dolerotheca reedana*, for comparison with fig. *1*. R—hollow resin rodlet. From coal ball Hb 208 A (t 4).

7—Peduncle (?) probably of *D. reedana*, showing vascular bundles. From coal ball Hb 208 B (B 4)

8—Vascular bundles shown in fig. 7, at higher magnification. Scale indicated at right.

9—*D. reedana*, bundle from near top of fructification for comparison with fig. *8*. From coal ball Hb 208 B (B 2), magnification same as fig. *8*.

derived by a process of telomic septation may conveniently be called a septangium. This and other self explanatory terms have been used in indicating possible lines of it be granted that the lygenopterid and medullosan pteridosperms, at least, have a common phyletic derivation and that the male fructifications in one or several of the

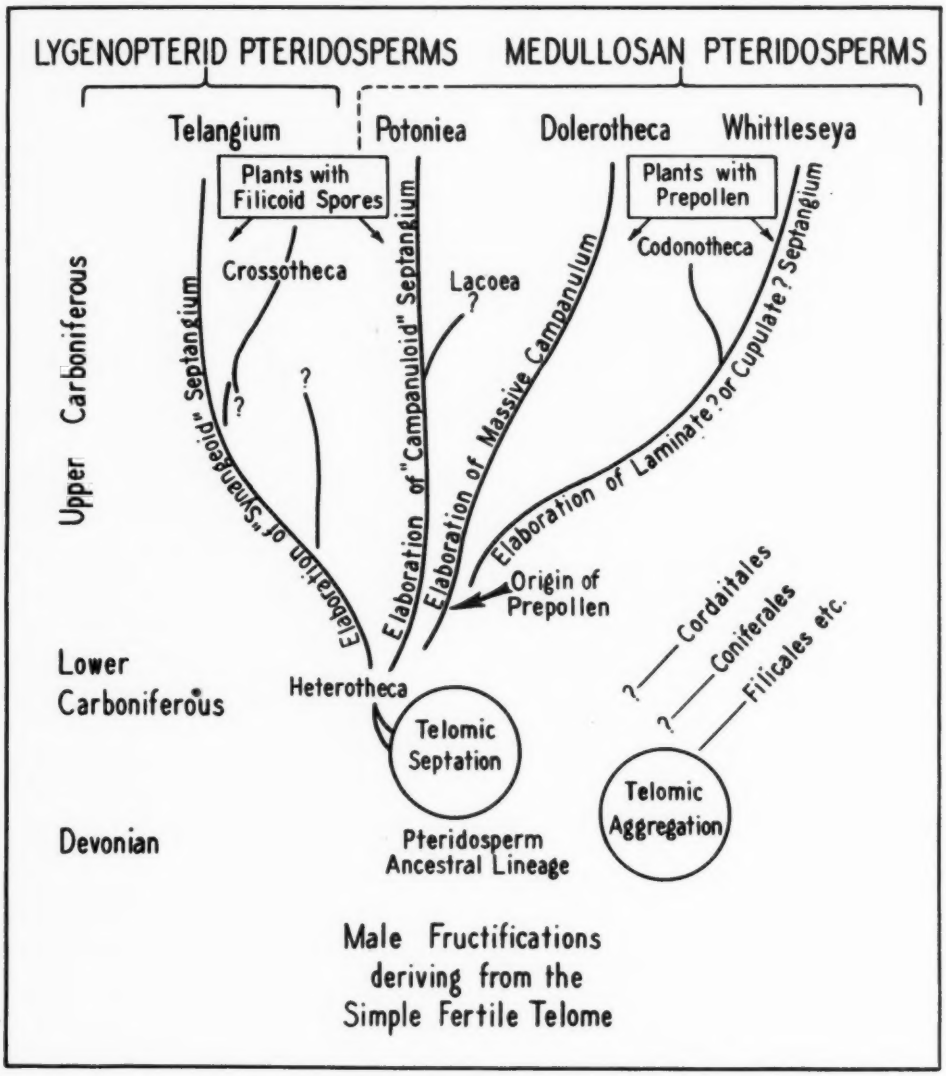


FIG. *17*—Hypothetical pteridosperm relationships according to septangial interpretation of male fructifications.

evolutionary morphologic modification in the chart given in text fig. 17.

The general problem posed in this connection may be briefly stated as follows: if constituent groups of this alliance had evolved by septangial modification, the possibility would be presented for extending the inference of telomic septation to the inter-

pretation of complicated sporangia in all of the pteridospermic groups. Although this question is highly theoretical, it could be of considerable importance in definition of the pteridosperm group as a whole. The suggestion of elaboration of pteridosperm male fructifications by the process of septation is not new, since Miss Benson recognized the distinct probability of its occurrence in at least two other important genera, as discussed below. The writer believes the septation hypothesis deserves more serious consideration than it has frequently been accorded in morphologic interpretation of the pteridosperm polleniferous structures.

The most surprising result of the present study, from the standpoint of comparative anatomy, is that *Dolerotheca* shows *no evidence of cyclic organization or derivation*. The radial arrangement of paired rows of sporangia is the dominating feature. Toward the margin new double rows of sporangia are intercalated; the new rows do not appear at any uniform distance from either center or periphery, but are inserted at various positions as the divergence between preexisting double rows affords space for their accommodation. Hence the symmetry of the *Dolerotheca* campanulum is decidedly radial in character and not cyclic. The symmetry is not very definite and the central focus of rows is not necessarily the center of the fructification.

In view of the fundamental importance which Dr. Halle has attached to cyclic arrangement in the Whittleseyinae, and the indisputable relationship between the Dolerothecineans and the Whittleseyineans, the morphology and morphogenetic derivation of the large pteridosperm fructifications may require reconsideration. To the writer, Dr. Halle's alternative suggestion, stated in the footnote on p. 57 of his important contribution on the spore bearing organs of pteridosperms, seems most easily reconciled with the present array of facts. He stated (Halle, 1933, p. 57 footnote), "It is perhaps also possible to imagine septation of a single sporangium of the remarkably large type found in some of the Psilophytales; the "sporangia" of *Sporogonites* have a certain superficial resemblance to the *Aulacotheca* type in shape, in their comparatively large size, and in their longitudinal furrows."

A synangial interpretation of *Dolerotheca* is difficult because *a pair* of tubular sporangia, rather than a single one that could be directly derived from a fertile telome, seems to be the fundamental unit of structure, and because the sporangial units, single or double, permit no easy comparative derivation from a telomic branch system (see Zimmerman, 1930). It would seem more plausible that the campanulum has been derived by septation or "septangy" and that *the whole fructification is comparable to a single telome*, much modified, rather than to a synangial aggregation of fertile telomes in the manner which was more strongly favored by Halle in 1933 and which he summarized in 1937. The process of sporangial septation is no more improbable, biologically, than the process of aggregation (synangy) in the case of fertile members. A basic evolutionary difference, involving synangy in ferns and septangy in pteridosperms, might, in fact, be called on to explain why the seed habit, with its various interconnected modifications, was so early attained by the latter group. The gymnospermic ovule represents an elaboration of a fertile telome also, and some degree of linkage is to be expected in male and female characteristics of the same plants.

It probably is not necessary to search as far back as the Devonian to find a primitive type of male fructification with plausible ancestral relationship to the Whittleseyas, Dolerothecas, and Potonieas, but the primitive type of telome is closely approximated in some of the Devonian plants. In the writer's opinion, the type of male fructification borne by *Heterotheca grievi* Benson, may serve very well to illustrate a plausible ancestor for *Potoniea*, *Whittleseya* and allied forms, and *Dolerotheca*.

Heterotheca was regarded as in biologic correlation (i.e., supposed to be a part of the same plant) with *Heterangium*, a genus identified by anatomical characteristics of the stem. Primitive species of *Heterangium* are about the proper geologic age and morphologic type to be close to the direct ancestry of both the Lyginopterid and Medullosan lines of pteridosperm specialization. Both *Heterangium* and *Heterotheca* are of Lower Carboniferous age from the Calciferous Sandstone in Scotland, and this fact

makes ancestral consideration feasible in relation to more specialized Upper Carboniferous (Pennsylvanian) forms.

The structure of *Heterotheca* is most readily interpreted as a product of sporangial septation (see Benson 1922, pp. 128–129). The fruiting body is slightly flattened, half-fusiform, and 3½ to 4 mm. long. It contains numerous sporangia, 16 of which may be seen in cross-section; 12 sporangia at the level shown in the cross section diagram, D, of the frontispiece, are peripheral and 4 central in position. The spores are small (20–30μ in diameter) with a trilete suture. A surface reconstruction of *Heterotheca* is also shown in fig. D of the frontispiece, drawn at the same scale as the *Dolerotheca* figures. The diagrammatic cross-section is drawn to a larger scale to indicate the relative locations of vascular bundles and sclerotic tissue.[9]

From such a structure as the *Heterotheca* fructification, it is possible to suggest several lines of evolutionary specialization, as is indicated in the schematic diagram in text fig. 17. No attempt has been made to present a complete pteridosperm synopsis in this chart, and gymnosperms other than pteridosperms are not included.

As to the possibility of complex fructifications arising by septation of simpler fertile structures, as well as by aggregation, Bower stated (Origin of a Land Flora, 1908, p. 111) "in each case of a synangium, it may be a question whether the structure results from septation or from fusion." Possibly nowhere in the plant kingdom does homoplasty play a more important part than in the development of the male fructifications of pteridosperms, and if the pteridosperms are truly one of the several large monophyletic plant groups the septate derivation of their male fructifications in general (in contrast to the aggregation interpretation of fern synangia) needs to be considered. Since it seems most essential to regard *Heterotheca* and *Dolerotheca* fructifications in this light, other genera definitely linked with Pteridosperms, such as *Crossotheca* and *Telangium*, also should be considered in the same fashion even though they more successfully simulate the synangia of ferns. Miss Benson has presented evidence for septate origin, both in her paper on *Telangium* (1904) and in her discussion of *Heterotheca* (1923).

In *Heterotheca* the internal sporangia are poorly placed for the shedding of spores; the development of elongate sporangia free of one another at the distal ends appears a likely evolutionary trend which is plausibly exemplified by *Telangium*. The frontispiece illustration, fig. E, shows a reconstruction of the *Telangium* fructification drawn at the same scale as the other figures. Other modifications of *Telangium* as contrasted with *Heterotheca* also are evident, but it seems necessary to call attention only to the contraction and simplification of the cover layer in *Telangium*, and to the elongation and reduction in number of characteristically *paired* sporangia.

In the derivation of *Potoniea* from a type like *Heterotheca*, it is evident that sporangia have been modified to tubular form and the fructification expanded. Whether they are anatomically paired or not, cannot be determined from the evidence at hand. The cover layer has been elaborated (rather than contracted as in *Telangium*) and evidently serves as a sporangial receptacle. The sporangia apparently are free of one another, at least for a considerable part of their length. This would represent a considerable improvement over the *Heterotheca* condition insofar as dispersal of spores is concerned. The great size elaboration of the *Potoniea* fructification is a significant feature.

Dolerotheca and *Whittleseya* and their closer relatives are distinguished from the pteridosperms previously mentioned in this connection, in having prepollen rather than fern-like types of spores. The suggestion has been made that these advanced spores may possess a vestigial third trilete ray; if so, they were derived from a tetrahedral tetrad

[9] Information about *Heterotheca* has been drawn entirely from Dr. Benson's publication of 1922. Reproductions of her original photographs illustrating this form do not offer very convincing support for the description or interpretation. Recently Dr. T. G. Halle, in a personal communication, has emphasized the need for further information about it. The writer sincerely agrees that a more definitive study, if possible with the aid of modern peel preparations, should be undertaken. Until this is done the accuracy of the original interpretation cannot be confirmed and opinions about the relationship of *Heterotheca* will have to be reserved to the extent, at least, of uncertainty about the photographic illustrations.

and thus may not differ as much as they would seem to at first glance, from the types of pteridosperms with fern-like microspores. Regardless of this, prepollen is sufficiently different from the matured androspores of the lygenopterid pteridosperms that an important biological difference is indicated. We are not in a position to interpret the full significance of prepollen as yet. A special pollenation mechanism seems to be implied, but at least the wide-spread occurrence of prepollen in the upper Paleozoic is well established.

Except for the important difference in spores, *Dolerotheca* and *Potoniea* show a similar tendency in elaboration of sporangia, and, to some extent, in enlargment of the campanulum as a whole. This structure in *Lacoea* is larger than in *Potoniea*, and compares more favorably in this respect.

Ground tissue completely enclosing *Dolerotheca* sporangia, and sclerotic tissue in the campanulary cover, are both quite plausibly derivative from the type of structure in *Heterotheca*. *Dolerotheca* shows more adequate provision for dispersal of spores.

The morphologic comparison of *Dolerotheca* and *Whittleseya* is clouded by what the writer believes must be a misinterpretation of the structure and organization in the latter. The previous ideas are reviewed briefly in order to clarify the present position.

Newberry (1853) adopted the view that the broad shovel-shaped organs (of which he had seen some thousands) were leaves of uncertain affinity. He evidently did not question their morphologic identity as leaves, but he was at a loss to relate them or place them systematically. Other authors substantially followed Newberry, more or less tentatively suggesting a gymnospermic alliance, until it became clear that these were fertile, rather than vegetative organs. Kidston may have been the first to suspect that they were the male organs of pteridosperms. A statement to this effect, somewhat unsatisfactory in details, was made by Seward (1917, p. 129) who illustrated prepollen Kidston had obtained from *Whittleseya elegans*. However, prior to Halle's study (1933), the tubular form of the sporangia, a most important characteristic, was unrecognized. Furthermore, Halle demonstrated that *two* rows of sporangia are present across the width of the *Whittleseya* "lamina."

Halle regarded the "lamina" essentially as a tube, containing "loculi . . . arranged in a uniseriate whorl," that owed its laminate form to compression. With this view the present writer is unable to agree.

The first occasion for doubting the cyclic arrangement of locules in *Whittleseya* fructifications came in the realization that it was entirely at variance with the radial organization shown by *Dolerotheca*. In other particulars it seemed possible to reasonably reconcile the new information on *Dolerotheca* with what was known about *Whittleseya*. It seemed strange that *Dolerotheca* should have sporangia radially arranged in paired rows, while in *Whittleseya*, very similar sporangia with similar spores, are arranged according to a wholly different unseriate cyclic pattern.

Further study and review of this matter haveconvinced the writer that the *Whittleseya* male fructification was never hollow, or campanuloid in form, but in truth is a laminar structure as it was first interpreted. He believes that it consists essentially of a single *paired* row of sporangia that is the morphological equivalent of one of the numerous paired sporangial rows so definitely established for *Dolerotheca*.

Such an interpretation appears to explain adequately all the features observed in Halle's excellent sections (new sections could hardly bear more definitely on this point because, as Halle stated, loc. cit., p. 22, "the median carbonized zone shows no natural longitudinal rupture nor any other indication that it has been formed by compression of two layers originally separated by a central cavity") and it likewise is in full accord with the extensive observations of Whittlesey (1849), Newberry (1853), White (1901) and others. Most of the specimens have been preserved in fine grained matrix that surely would have filled any hollow central cavity in some instances, had such a cavity ever existed. The very thin intervening shale layer Halle demonstrated at the distal edge of the lamina is not at all commensurate with the hollow cavity he postulated, and possibly it may be related to a dehiscence groove similar to those of *Dolerotheca*. There is no specimen known to the writer, nor any that has been described,

in which such a central filling is a prominent feature. A quotation from Whittlesey's little-cited original description (1849) of the *Whittleseya elegans* fructification is still most pertinent to the discussion:

> It was first observed by my brother, the Rev. S. H. Whittlesey, about four years ago in the falling roof of the "Chestnut Ridge" coal mine, discovered and opened by us in 1845, and which is situated one mile and a quarter northwest by north from the centre of Tallmadge, Summit County, Ohio.
>
> It is there called "the flower," and has a striking general resemblance to one, but has no botanical resemblance to flowers or other parts of fructification.
>
> If this was originally an *open pod* whether a flower or not, there should have been seen among several hundred specimens that I have examined, evidences of a circular or oval opening at the edge or apex of the figure. These edges could not always have been pressed together symmetrically so as exactly to cover each other, and if there were two surfaces with interior organs between them, it must have occasionally appeared in that light. But in no instance is there such a separation of the serrated edges, there being but one line across the apex, which is generally straight or slightly curving, as in the drawing.
>
> . . . The very fine but distinct curved lines or striae, extend with great regularity, converging to a point at the base where the stem unites. Its space in the rock is represented by a *very thin* scale of coal, the raised lines on one face of the specimen corresponding to depressed lines on the counterpart, showing it to be a single thickness and not double.
>
> . . . On some of them may be seen fine cross marking like nerves of reticulation, but in the finest specimens these are wanting, and are probably due to wrinkles of compression. The teeth at the edge are not uniform in number. I have counted from eighteen to twenty-six. The light, slender, but well defined stem is generally wanting. It is never seen longer than represented in the sketch, and seldom more than half an inch in length, where it terminates abruptly as though it were broken off. There are minute straight lines like fibres in this stem.
>
> (The fossils) . . . exist in the ordinary bluish gray, soft argillo-siliceous shale of the coal series, and in spots are seen in immense numbers, from one to one and half feet above the coal. The shale is charged with myriads of coal plants, but the only hint I have met with showing any relation between this and the other plants, is the fact that where the *Pecopteris lonchitica* is most abundant, this is seen in greatest numbers.
>
> . . . The *Carpolithus* is abundant in the roof of the same mine.

It will be noted that the most striking feature of Halle's reconstruction (loc. cit., text fig. 5, p. 24), viz., the duplicate distal margin of the hollow bell, is the feature Whittlesey stated is never seen although he quite evidently looked carefully for such an indication. In several respects Whittlesey's discussion is more astute than that of later authors; he certainly was impressed with the possiblity that the organs might be fertile structures. Halle's modern study has fully confirmed Whittlesey's suspicion as to the nature of the organs, but is not reconciled with the general evidence as to their morphology. All facts known now appear in reasonable agreement if the view expressed regarding the paired sporangial row is adopted; further information on sporangial dehiscence and tissue structure is not likely to be obtained until petrified specimens are found.

The morphology of these organs naturally has important bearing on their phyletic morphogenesis. For the same reasons that the writer questions the cyclic arrangement of *Whittleseya* sporangia, he also questions that such organs can be derived from "a whorl of fertile telomes fused tangentially" (cf. Halle, 1937, p. 231).

Although the *Whittleseya* fructification is not nearly as massive as that of *Dolerotheca*, the probable correspondence in plan of organization argues about as strongly for a septangial interpretation of one as the other. It appears that the cover layer of *Whittleseya* has been persistent, but that the fructification has enlarged along two radii only, instead of many. Neither the radial nor bilateral symmetry of *Dolerotheca* is exact, but the *Whittleseya* fructification may be more nearly symmetrical bilaterally. The fact that *Heterotheca* fructifications are not perfectly half-fusiform, but show a bilateral tendency in transverse outline, suggests the possibility of deriving a more strictly bilateral fructification from it as well as a more massive radial type. There is little question that significant differences of long standing exist between *Dolerotheca* and *Whittleseya*, and it is supposed that the parent stocks diverged at a fairly early date, after prepollen was an established feature, as indicated in text figure 17.

In *Codonotheca* the cover layer appears to have become contracted to expose the free ends of sporangia. Such development would seem a parallelism of that which took place earlier and more directly in the ancestry of

Telangium. It is interesting that *Codonotheca* is of large size and that no reversion to the fern-simulating septangial type has occurred.

The writer believes that although the phyletic relationships and postulated structural modifications are highly speculative, they have greater likelihood of substantiation, in part at least, than may frequently be the case in a "Merkmals Phylogenie" (see Zimmerman, 1930). This belief is based on convergence of evidence supplied by the probable biologically correlative fossils (stems, leaves, seeds) which can not be discussed in this paper. Many of the relationships, of course, are not likely to be satisfactorily established for many years.

It appears that such matters of phylogenetic relationship as have been suggested may have an importance beyond their inherent theoretic interest. The elaboration of the male fructifications very probably occurred as a gradual evolutionary process in many linked characteristics. If a "key" can be supplied to gradational evolutionary series in geologic time, it provides a most convenient tool for the stratigraphic paleontologist wherever such fossils are encountered. The evolutionary hypotheses embodied in the foregoing discussion should be tested wherever possible by comparison with other better known fossils, to indicate more objectively their value in stratigraphic definition. Their value as time indices will be more evident as discernible stages of evolutionary development are keyed with definite stratigraphic zones. The male organs discussed here have the advantage (from the paleontologic standpoint) of a fairly determinate type of growth, so that in normal course of fossil preservation, typical specimens should be mature and therefore fairly comparable ontogenetically.

ACKOWLEDGMENTS

All this investigation was conducted and much of the manuscript written in 1939–1941 while the author was employed by the Illinois Geological Survey. The writer is indebted to many members of the staff of the Illinois Geological Survey for aid in completing this paper for publication. Gilbert H. Cady, Head of the Coal Division, has offered encouragement and very material assistance in critically reviewing the manuscript. Many of the sections of *Dolerotheca* were prepared by Allen Platt under the writer's supervision. The final drawings of surface reconstructions included in the frontispiece, and of the detailed drawings from sections of the fructifications were made by Daniel M. Morgan, now employed by the U. S. Weather Bureau at Alliance, Nebraska. Robert M. Kosanke, Paleobotanist of the Illinois Geological Survey, assisted in many ways.

The writer wishes to express his appreciation to all who have assisted him, and particularly to M. M. Leighton, Chief, for his continuing interest and support in these investigations.

REFERENCES

ANDREWS, H. N., 1945, Contributions to our knowledge of American Carboniferous floras. VII. Some pteridosperm stems from Iowa. Missouri Bot. Garden Annals, vol. 32, pp. 323–360.

ARNOLD, C. A., 1937, The seeds of *Alethopteris*, and other pteridosperms from North America. Deuxième Congrès pour l'Avancement des Études de Stratigraphie Carbonifère, Heerlen, 1935, Compte Rendu, vol. 1, pp. 41–45.

BENSON, MARGARET, 1904, *Telangium scotti*. Annals of Botany, vol. 18, pp. 161–177.

——, 1922, *Heterotheca grievii*. The microsporange of *Heterangium grievii*. Bot. Gazette, vol. 74 (2), pp. 121–142.

BOWER, F. O., 1908, Origin of a land flora. pp. 1–727, Macmillan, London.

DARRAH, W. C., 1937, *Codonotheca* and *Crossotheca:* polleniferous structures of pteridosperms. Harvard Univ. Bot. Mus. Leaflets, vol. 4 (9), pp. 153–172.

DAWSON, J. W., 1890, New plants from the Erian and Carboniferous and on characters and affinities of Paleozoic gymnosperms. Canadian Rec. of Sci., vol. 4 (1) Jan., pp. 1–28.

FLORIN, RUDOLF, 1925, Zur Kenntnis der Paläozoischen Pflanzengattung *Dolerophyllum* Saporta. Svensk. bot. tidskr., vol. 19, pp. 171–191.

——, 1925, Zur Kenntnis einiger Cyclopteriden des Oberkarbons. Geol. fören. Stockholm Förh., vol. 47 (2), pp. 223–244.

——, 1926, Über einige Blätterabdrucke vom Cyclopteris-Typus aus dem Karbon und Perm. Arkiv för Botanik, vol. 20 A (13), pp. 1–19.

——, 1937, On the morphology of the pollen grains in some Paleozoic pteridosperms. Svensk. bot. tidskr., vol. 31 (2), pp. 305–338.

HALLE, T. G., 1929, Some seed-bearing pteridosperms from the Permian of China. K. svenska vetensk. akad. Handl., tredje serien 6 (8), pp. 1–24.

——, 1933, The structure of certain fossil spore-bearing organs believed to belong to pteridо-

sperms. K. svenska vetensk. akad. Handl., tredje serien, 12 (6), pp. 1–103.

——, 1937, The position and arrangement of the spore-producing members of the Paleozoic pteridosperms. Deuxième Congrès pour l'Avancement des Études de Stratigraphie Carbonifère, Heerlen, 1935, Compte Rendu, vol. 1, pp. 227–235.

GRAND'EURY, F. C., 1877, Flore Carbonifère du départment de la Loire et du centre de la France Mem. présentés par divers savants á l'Academie des sci. de l'Institut de France. Extrait du Tome XXIV. Text, pp. 1–624. Pub. by J. Baudry. Atlas, 34 pls.+map. Paris.

——, 1890, Geologie et Paleontologie du bassin Houiller du Gard. Text, pp. 1–354, St.-Étienne. Atlas, pls. 1–22, Paris and St.-Étienne.

HOSKINS, J. H., 1923, A Paleozoic angiosperm from an American coal ball, Bot. Gazette, vol. 75, pp. 390–399.

NEWBERRY, J. S., 1853a, Fossil plants of the Ohio coal basin [a catalog listing]. Annals of Science (Cleveland), vol. 1 (8), pp. 95–97; (9), pp. 106–108.

——, 1853b, New fossil plants from Ohio (1). Annals of Science (Cleveland), vol. 1 (10), pp. 116–117.

READ, C. B., 1946, A Pennsylvanian florule from the Forkston coal in the Dutch Mountain outlier, northeastern Pennsylvania. U. S. Geol. Survey Prof. Paper 210-B, pp. 17–28, Washington.

RENAULT, BERNARD, 1896, Bassin Houiller d'Autun et d'Epinac. Études des Gîtes Minéraux de La France, fasc. IV, atlas 1893; text.

——, 1902, Note sur quelques Micro et Macrospores Fossiles. Soc. d'Histoire Nat. d'Autun Bull., vol. 15, pp. 67–118.

SCHOPF, J. M., 1938, A significant collection of American coal balls, Chronica Botanica IV, pp. 184–185.

——, 1938, Spores from the Herrin (No. 6) coal bed in Illinois. Illinois Geol. Survey Rept. Inv. No. 50, pp. 1–74.

——, 1939, *Medullosa distelica*, a new species of the Anglica group of *Medullosa*. Am. Jour. Botany, vol. 26, pp. 196–207.

——, 1941, *Mazocarpon oedipternum* and sigillarian relationships. Illinois Geol. Survey Rept. Inv. No. 75, pp. 1–54.

——, WILSON, L. R., and BENTALL, Ray, 1944, An annotated synopsis of Paleozoic fossil spores and the definition of generic groups. Illinois Geol. Survey Rept. Inv. No. 91, pp. 1–74.

SAPORTE, GASTON DE, and MARION, A.-F., 1885, L'Évolution du règne végétal. Les phanérogames, vol. 1, pp. 1–249, Baillière, Paris.

SELLARDS, E. H., 1903, *Codonotheca*, a new type of spore-bearing organ from the coal measures. Am. Jour. Sci., 4th ser., vol. 16, pp. 87–95.

——, 1907, Notes on the spore-bearing organ *Codonotheca* and its relationship with the Cycadofilices. New Phytologist, vol. 6, pp. 175–178.

——, 1908, Fossil plants of the Upper Paleozoic of Kansas. Kansas Univ. Geol. Survey, vol. 9, pp. 386–480.

SEWARD, A. C., 1917, Fossil plants, vol. III, Cambridge Univ. Press.

——, 1923, A supposed Paleozoic angiosperm. Bot. Gazette, vol. 76, p. 215.

STEIDTMANN, W. E., 1944, The anatomy and affinities of *Medullosa noei* Steidtmann, and associated foliage, roots and seeds. Michigan Univ., Mus. Paleontology Contr., vol. 6 (7), pp. 131–166.

WHITE, DAVID, 1901, The Canadian species of the genus Whittleseya and their systematic relations. Ottawa Naturalist, vol. 15 (4), pp. 98–110.

——, 1903, Summary of fossil plants recorded from the upper Carboniferous and Permian formations of Kansas. U. S. Geol. Survey, Bull. 211, pp. 85–117.

WHITTLESEY, CHARLES, 1849, Description of a coal plant supposed to be new. Am. Jour. Sci., 2d ser., vol. 8, pp. 375–377.

WILSON, C. L., 1937, The phylogeny of the stamen. Am. Jour. Botany, vol. 24, pp. 686–699.

WODEHOUSE, R. P., 1935, Pollen grains. Their structure, identification and significance in science and medicine. Pp. 1–574, McGraw-Hill, New York.

ZIMMERMAN, WALTER, 1930, Die Phylogenie der Pflanzen. Pp. 1–454, Gustav Fischer, Jena.

JOURNAL OF PALEONTOLOGY, VOL. 22, NO. 6, PP. 725–761, 23 TEXT FIGS., NOVEMBER 1948

STUDIES IN QUANTITATIVE PALEONTOLOGY: I. SOME ASPECTS OF THE THEORY AND PRACTICE OF QUANTITATIVE INVERTEBRATE PALEONTOLOGY

BENJAMIN H. BURMA
University of Nebraska, Lincoln, Nebraska

ABSTRACT—For some time there has been a noticeable trend toward a more strictly quantitative outlook in paleontology. In view of many special circumstances encountered in dealing with fossil material, there is a rather extended consideration here given to the theoretical background of the quantitative method as applied to fossil invertebrates. First there is a consideration of the relations between sampling theory and paleontology. This is followed by a discussion of variability in populations and the problem of inference from sample to population. A consideration is next given to the species concept and a comparison of the units which can be used by the paleontologist to those used by the neozoologist. The problem of distinguishing between two species is then considered, this being done from several aspects. Synchronous species, a source of much difficulty, are discussed at some length and this leads into the problem of geographic gradients or clines. This in turn brings up the subject of infraspecific units and the possibility, and advisability, of recognizing them. There is also a short discussion of methods of presentation of data. The last part of the paper deals with the practical application of these various methods to the study of several representative kinds of invertebrate fossils. Of these, the blastoids are representatives of animals that build skeletons of plates, the pelecypods and brachiopods of those with two valves. There are two general types of spiral shells, that in which the initial portion is not enclosed within the later portion, and that in which it is. The gastropods serve to represent the first type, and the fusulinids the second.

It is concluded that quantitative methods are demanded by theoretical considerations and that they are thoroughly usable and practical.

THIS paper is the outgrowth of some ten years of work devoted to the problem of how to get the most, and the most accurate, information from paleontological materials. As a result of this study, it has been concluded that quantitative methods represent the best approach. However, a rather extended search of the literature has failed to reveal any statement of the theoretical and philosophical background for such studies which would also take into consideration the special problems encountered in dealing with invertebrate fossils. The growing trend toward the quantitative outlook in the field of invertebrate paleontology makes the need for such a statement imperative.

HISTORICAL REVIEW

It is beyond the scope of this paper to deal with the development of the quantitative attidude in science. In any branch, the qualitative outlook has been the mark of its youthful stages, and the assumption of a quantitative outlook has marked the beginning of maturity. Invertebrate paleontology to date has been almost entirely qualitative. A few students have made some use of quantitative methods but practically none has used them consistently or fully.

The British have probably used quantitative techniques most. Among the earlier workers was Carruthers (1910) who has been widely followed by other British coral students. His studies are, however, best termed semi-quantitative. A. E. Trueman (1922) used frequency graphs to show the evolutionary changes in *Gryphaea*. In 1924 (Trueman, 1924), he published a short paper on the species concept in which he concluded that the species name is best applied only to those specimens which agree with the characters of the holotype and that variations should be otherwise distinguished. This abiological concept of the species was used by Davies and Trueman in their 1924 publication on the Coal Measures lamellibranchs. This paper makes use of frequency

plots, scattergrams, and coefficients of correlation to show the variability of populations. In the late 1920's two papers appeared on the ontogenetic variation in gastropods (Stuart, 1927; Rowlands, 1928). These emphasized the importance of variation in ontogenetic development, but such a beginning does not seem to have been further developed. Waddington (1929) urged the use of more strictly quantitative methods in the study of ammonites but his recommendations likewise do not seem to have been much followed.

Willard (1930) published a short paper on the evolution of the Platystrophias. He used averages of characters but his data were not analyzed and variation was largely ignored. As a consequence his conclusions are open to question. Elias (1937) dealt with the late Paleozoic fenestrate bryozoans using some quantitative measures with, apparently, much success. Here again, however, the data were not analyzed and little attention was paid to variation. Leitch (1936, 1940) has written concerning the Coal Measures lamellibranchs. His 1940 paper, particularly, includes statistical analyses and is an important advance because it defines species in terms of variation.

Simpson has written a number of papers dealing with the quantitative aspects of paleontology, particularly vertebrate paleontology. His book on methods (Simpson and Roe, 1939) is invaluable to the interested paleontologist. Salmon (1942) has made some use of quantitative methods, but her treatment of the Mohawkian Rafinesquinas is essentially qualitative. Nicol (1944) has published a study of *Elphidium* made on a strictly quantitative basis. This paper, excellent in concept, is discussed at some length below. The year 1945 saw a number of such papers published. Bancroft's (1945) very important posthumous paper on brachiopods made full use of symbols in a quantitative manner, seemingly with great success. C. L. Cooper (1945) presented a quantitative approach to the study of moult-stages of ostracodes using ontogenetic formulae. Schenck (1945) attempted to study the shifting of populations during the late Tertiary on the Pacific coast with reference to their present distribution, but encountered difficulties due to lack of distributional and other data. Wood and Barnard (1946) have published a very exhaustive study of the variation of *Ophthalmidium* but their approach was essentially qualitative. Finally there is the recent paper of Jeffords (1947) on late Paleozoic lophophyllid corals which is tantalizing because of its suggestion of the possible applications of truly quantitative methods to the study of corals.

The above review makes no pretense to completeness but constitutes a fair sample of the papers and emphasizes the recency of such studies and the increasing amount of attention given them. Other papers are discussed later in this study.

OBJECTIVES

The present paper is an attempt to make a rather thorough inquiry into the theoretical and philosophical basis for quantitative work with fossil invertebrates, and into some typical applications of these methods. Proportionately more space is devoted to the theoretical than to the purely practical aspects of the subject.

Only minimum attention is given to statistical methods in this paper. For persons without a mathematical background, Simpson and Roe's "Quantitative Zoology" is excellent as a reference. Those with a mathematical background will find Fisher's "Statistical Methods for Research Workers" useful. Methods discussed in these books are referred to throughout this paper. The theoretical discussions, however, are made as non-mathematical as is consistent with clarity and usefulness.

Great difficulty has been experienced in the organization of this paper. Most of the subjects discussed presuppose a knowledge of so many others that it has been impossible to avoid a great deal of cross-reference. Also the present study is concerned with species and infraspecific units only. Generic and higher units are more or less arbitrary groupings which are not particularly amenable to quantitative handling.

ACKNOWLEDGEMENTS

Financial assistance has been rendered this study by the Wisconsin Alumni Research Foundation of the University of Wisconsin and is gratefully acknowledged. I wish particularly to express my great debt

to Dr. Norman D. Newell who early encouraged me in these studies. Drs. Lewis M. Cline and M. L. Thompson have given me the benefit of stimulating criticism. Dr. K. J. Arnold has contributed much excellent advice concerning statistical methods but responsibility for their manner of use in this paper is entirely my own.

SAMPLING THEORY AND PALEONTOLOGY

A fundamental factor in any consideration of the quantitative approach to paleontology is embodied in sampling theory. Before discussing some of the consequences of this theory, it may be well to review it briefly.

The primary interest in paleontology is, or should be, the study of fossil populations. However, it is quite impossible to study all the members of a population. Only part of the original population was preserved, of this some specimens have been destroyed and most of the remainder are unavailable because they are buried beyond reach. Also it is a sheer impossibility to carefully observe the enormous number of individuals that may be available. For these reasons, it is necessary to study a comparatively small number of specimens, a sample, selected from a population. From the study of this relatively small sample we seek to infer the properties of the population from which it was drawn, and further, to infer the probable character of other samples that may be drawn from this same population.

Obviously, the best sample would be one in which the entire range of variation present in the population is represented, and in the same proportions. If we were allowed a sufficiently large sample and could select the individuals in it, we might hope to come very close to this desideratum. In actual practice, neither of these two conditions can be met. Samples studied are, for one reason or another, mostly small, and clearly we cannot select specimens to show the nature of a population when it is that nature which we wish to determine. This means that samples, being unselected, may or may not correspond closely to the population. Under these circumstances, which are unavoidable and must be accepted, our inferences may be widely in error.

In practice, a sample is usually taken by going to an outcrop and picking up whatever specimens are available. Under the circumstances, this is the best method of sampling, for the sample will then be as nearly random as possible. (Actually, of course, the random-ness of the sample may be altered by conditions obtaining at the time of burial of the fossils. This is an inherent difficulty which cannot be overcome. Our object should be to avoid adding any additional selection.) The word "random" as used in this sense is rather difficult to define, and a rigorous definition will not be attempted here. Essentially, it means that, within available limits, no element of the population will be favored over another. For example, we will not study the larger members of a population and avoid the smaller ones. If we did, our sample would not be random, and our view of the population would be correspondingly distorted.

The fact that a given sample is random does not mean that any other sample drawn from the same population will have precisely the same characteristics. In fact, the opposite is true. If we have a population of 500,000 white and 500,000 black organisms (two independent characters) which are thoroughly mixed (a homogeneous population), a random sample of six would not invariably consist of three white and three black individuals. Actually, in the long run, a series of 64 samples of six specimens each would have this composition:

6 black	1 sample
5 black, 1 white	6 samples
4 black, 2 white	15 samples
3 black, 3 white	20 samples
2 black, 4 white	15 samples
1 black, 5 white	6 samples
6 white	1 sample

Thus the proportions of two independent variables will reflect the composition of the entire population exactly in less than one-third of the samples consisting of six individuals. As the number of independent variables increases, this correspondence drops rapidly. If we take a sample of six from a homogeneous population of three independent variables, only about 1/11 of the samples will have the same compositions as the original population. The actual situation, however, is not quite so unsatisfactory because most characters of animals are not

independent but are correlated and they tend to vary together according to certain definite proportions. This means that an average sample will come closer to approximating the original population. The general conclusion, however, still holds true. Any two samples taken from a population cannot be expected to be exactly similar and probably they will not be.

To consider only one variable: A fundamental problem in paleontology is the comparison of two collections, or better, two samples. We wish to know, usually, if these two belong to the same species (might have been drawn from one population), or if they belong to different species (probably came from two separate populations). The fact that collections are samples of populations has, with few exceptions, been ignored and investigators have proceeded on the false and unwarranted assumption that collections are in fact perfect reflections of the populations they represent. We have just seen that the fact that two samples differ, even widely, does not necessarily mean that they came from different populations. On the contrary, we should expect that two samples from the same population will differ from each another. Many paleontologists, past and present, seem however to have proceeded on the assumption that the species is an entity which admits little or no variation. It is as though they subconsciously appealed to the old idea of "archetypes" and considered that there is some basic, metaphysical model to which the members of a species must conform. Thus, each time they obtained a group of specimens, or even a single individual which varied, often even slightly, from the holotype, they forthwith described another "species." The analysis above, and that which follows, should indicate clearly that such procedure is, to put it most kindly, suspect. We can only conclude that all "species" created under the aegis of qualitative paleontology are to be viewed with great suspicion. Many are undoubtedly valid groups; many more were as certainly created on inadequate grounds. The mere fact that two collections, or two parts of a single collection differ in their composition is not an *a priori* reason for concluding that they were drawn from different populations.

VARIABILITY

Variability may be somewhat loosely defined as the tendency of one individual to differ from others in the same population. Its relative and actual amount will itself vary from character to character within a single species and from one species to another. Although the limits of variation are wide, we may expect that, in general, the maximum value of any character will be about 50 per cent greater than the minimum value for any particular growth stage. As an example, if the minimum width of a brachiopod at a certain growth stage is six mm., the maximum width may be expected to be about nine mm. It must be emphasized that this amount of variation is not unusual, but entirely normal. In fact, if the variability of a good-sized sample is too low, it is generally an indication that sampling has been inadequate or selective. In spite of these facts, it is commonplace for individuals at one end of a variable series to be separated from individuals at the other end, and perhaps both from the more abundant middle members of the sample, and considered to represent two, three or more "species" instead of one. There is no simple method for dealing with this problem. If the sample is sufficiently large, the intergradation of forms will usually be obvious, and generally there will be few representatives of either extreme with more and more intermediate specimens as the middle part of the range is approached (a normal distribution). If two well-marked frequency maxima are found, it may be an indication that two populations are represented in the sample. Only rarely, however, will paleontological samples be large enough to show this clearly. Usually sampling errors will confuse the situation so that no such simple separation is possible. An actual case is described below in the section on the Blastoidea.

Usually it is well to make the preliminary assumption that only one species of any genus is present in a sample. In modern marine faunas two very similar species do not commonly exist side by side, although such associations are certainly known. This problem is considered further below.

With these factors in mind, let us see what kind of units we *can* recognize, regardless of the label we place on them, as opposed to

what kind of units we might *like* to recognize. Assume that we have collected a suite of some particular kind of fossil from a homogeneous population. This sample will have certain individual characteristics. It will consist of a certain number of individuals (N). It will have a certain arithmetic mean, or, simply, a certain mean[1]

$$\frac{\Sigma X}{N}.$$

It will show a certain variability, which almost certainly will not exactly duplicate variability of the population from which the sample was drawn. It will have a certain standard deviation

$$\left(\sqrt{\frac{\Sigma(d^2)}{N}} \quad \text{or} \quad \sqrt{\frac{\Sigma(X^2)}{N}-\left(\frac{\Sigma X}{N}\right)^2}\right.$$

in which d is the difference between the measured value of a character in a single individual and the mean of the sample, or, in statistical language, the deviation from the mean.

So far we have considered only the sample. Our real interest, however, is, or should be, the population of which the sample is a part. In qualitative paleontology, inferences from sample to population are made on the basis of opinion. Unfortunately, opinions are widely variable, and still more importantly, one person has no way of checking another's opinion because it is wholly subjective.

There can be no effective argument against the injection of objective, quantitative methods into such a haphazard state of affairs. Fortunately, relatively simple methods exist for attacking this problem. The standard deviation (σ), just referred to, is a measure of the central tendency of a sample, i.e. the tendency for its members to group themselves about a mean. The smaller the value of σ, the less variable the sample is and the larger its value, the greater the variability. Further, if the sample (and population) approaches a normal distribution, as most do, we may calculate the expected limits of variability to any desired degree of accuracy. For example, for a sample with mean, M:

$M \pm 1\sigma$ includes 68% of the population
$M \pm 2\sigma$ includes 95.5% of the population
$M \pm 3\sigma$ includes 99.7% of the population
$M \pm 4\sigma$ includes 99.994% of the population

Thus, if the mean of a sample is 30 mm. and its standard deviation is 4 mm., only three individuals in a thousand of the original population should fall outside the range of 18 mm. to 42 mm. ($M \pm 3\sigma$). Thus, with the usual margin for error that we must always leave when dealing in probabilities, we may say that our population varies in size from 18 mm. to 42 mm. for one particular growth stage. The value $M \pm 3\sigma$ is most commonly used for this purpose and is generally adequate. Simpson (1941) offered some cogent criticisms of this method which are dealt with in the next section.

After inferring the limits of a population, we are next concerned with its mean. Although the mean of the sample, or the "typical specimens," is practically a fetish among many paleontologists, it is not as useful or characteristic a feature of the population as its variation. However, because of its wide usage and because it is more easily and widely understood than measures of variability, it is considered throughout this paper. Only by pure coincidence will the mean of a sample correspond exactly with the mean of a population. If, however, the standard deviation be divided by the square root of the number of individuals in the sample ($\sigma/\sqrt{N}$), a measure known as the standard error of the mean (σ_M) is obtained. If this measure be added to and subtracted from the mean in the same fashion as the standard deviation, we obtain the range within which the mean of the population may be expected to fall, to any desired accuracy. Thus, if $M = 50$ mm. and $\sigma_M = 0.5$ mm. ($3\sigma_M = 1.5$ mm.), the chances are 997 in 1000 that the mean of the population will fall in the range from 48.5 mm. to 51.5 mm. The converse is also true: With the same sample, the mean of the population *cannot* be determined more closely than to say that it probably lies between 48.5 mm. and 51.5 mm. This is extremely important.

[1] The symbols used here are those of Simpson and Roe (1939). The symbols used by Fisher and other statisticians differ somewhat. X is the individual measure of one character of one specimen.

THE SPECIES CONCEPT

The definition of the word "species" has been the subject of a great deal of debate, much of it, unfortunately, rather fruitless. Perhaps the best recent discussion of the word and concept is by Mayr (1943, p. 102 *et seq.*) He concludes by defining the species as: "a group of populations which replace each other geographically or ecologically and of which the neighboring ones intergrade and interbreed wherever they are in

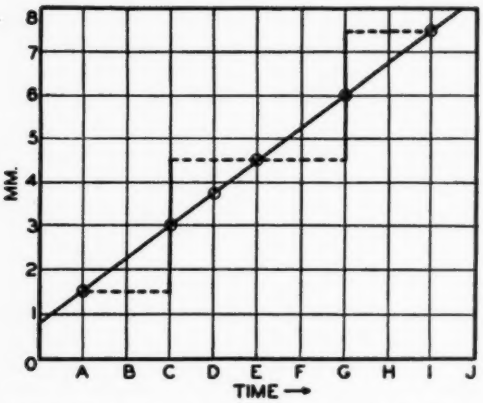


FIG. *1*—Diagram showing the theoretical range of a species.

contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers. Or shorter, species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups." This definition seems to be an excellent one for the neozoologists. For the paleontologists, it is inadequate. Obviously we cannot view two similar specimens dead for millions of years and determine whether they belonged to interbreeding populations, potentially or otherwise. If those parts dealing with interbreeding are eliminated from Mayr's short definition, we are left with "species are groups of . . . natural populations . . . ," which is hardly a helpful statement. Not being able to use a strictly biological definition of the species, we are forced, therefore to turn to a morphological definition with its attendant difficulties which Mayr has pointed out.

Most geneticists, zoologists, and paleontologists now agree that animal evolution has been an essentially continuous process unmarked by major saltations (Dobzhansky, 1941; Mayr, 1942; Simpson, 1944). As such, its course is better represented by a continuous line than by a series of *en echelon* line segments. This conclusion cannot be reviewed here but is accepted as the basis for the continuation of the present discussion.

Continuous evolution, however, introduces a difficulty when we come to define species. How can we distinguish stages in what is a continuous process? To set up a division at any point must be purely arbitrary. But species, as they have been distinguished, are set up as stages in this continuous evolutionary line. We are thus forced to the conclusion that "species" is a concept without objective existence when populations are viewed in a four-dimensional continuum.

On the other hand, we must also admit that the human mind is uncomfortable in dealing with continuities and is most at home with easily handled, discrete units. Our first effort should, therefore, be to decide how best to distinguish such units—which we will hereafter term "species." We have seen that we can infer the total range of the variation and that of the mean of a given population. Either of these ranges could be used for our present purpose but for reasons mentioned above, the range of the mean seems most suitable.

Let us now consider a phyletic line illustrated by the rising line in figure 1. In beds of age *C* we find fossils belonging to this evolutionary line. The mean of the sample falls, let us say, on the line at size 3.0 mm., and we find the standard error of the mean (σ_M) to be 0.50 mm. As we have already seen, we might expect the mean of the population to fall between 1.5 mm. and 4.5 mm. Now suppose we find fossils of the same evolutionary line in rocks of age *D*, the mean of its sample being 3.8 mm. and σ_M also 0.50 mm. According to our analysis of population *C*, its mean could be anything between 1.5 mm. and 4.5 mm. and the sample from *D* has its mean within this

range. This indicates that populations *C* and *D cannot* be distinguished.[2] In fact only in rocks older than age *A* and younger than age *E* would we expect to find samples which we can justify separating from population *C*. Such a unit may be designated a species insofar as paleontology is concerned. Thus, we might recognize species 1 with time range *A* to *E* and character range 1.5 mm. to 4.5 mm. and species 2 of time range *E*, to *I* and character range 4.5 mm. to 7.5 mm. Actually, as already intimated, the method above needs modification to be more accurate. First, since we are making a prediction and are working with only one sample, we must assume that any other sample we will compare to ours will be of the same size and have the same standard error of the mean. Since the two will belong to the same phyletic line, this last is not unreasonable. Under these circumstances, the expression

$$\sigma_d = \sqrt{\frac{N_1}{N_2}\sigma_{M_1}^2 + \frac{N_2}{N_1}\sigma_{M_2}^2}$$

reduces to

$$\sigma_d = \sqrt{2\sigma_M^2}.$$

This last expression is then used instead of σ_M. Our expression for the range of the species then becomes,

$$\text{range} = M \pm 3\sqrt{2\sigma_M^2}.$$

On this basis, we can objectively set up the limits within which we will refer several populations to the same species.

ONE OR TWO SPECIES?

A problem constantly confronting the paleontologist is that of deciding whether the collection (sample) he is working with belongs to some already described species or whether it is different. In the past, this question has been answered on a variety of bases, none of them particularly satisfactory. Commonly the decision was simply an opinion but such a haphazard method is to be defended only on the shaky grounds of expedience. Essentially our problem involves the comparison of two samples; one, our particular sample, and the other, the species with which we wish to compare it. Three general means of attack are open to us; a comparison of one character of each at a time; a comparison of two characters at a time; or a comparison of all relevant characters at once. These are discussed in order.

The few quantitative comparisons of invertebrate fossils have been made almost solely on the basis of single characters. There are several ways in which this can be done. An excellent one is that of the comparison of means by the following method: σ_d is calculated from either

$$\sigma_d = \sqrt{\frac{N_1}{N_2}\sigma_{M_1}^2 + \frac{N_2}{N_1}\sigma_{M_2}^2} \quad \text{or} \quad \sigma_d = \sqrt{\frac{\sigma_1^2}{N_2} + \frac{\sigma_2^2}{N_1}}$$

whichever is most convenient. Next d is obtained by subtracting the smaller arithmetic mean from the larger. Then d is divided by $\sigma_d \cdot (d/\sigma_d)$. If the resultant is less than 2.0 ($P = 0.956-$), the difference between the means is probably not significant, this probability increasing rapidly as the number decreases. If the answer is between 2.0 and 3.0 ($P = 0.955$ to $P = 0.997$) the difference is possibly significant. If the result is 3.0 or more ($P = 0.997+$), the difference is almost certainly significant, the degree of probability increasing rapidly with the increase in the number. If the samples compared are small (say 20 or less), the quantity t may be calculated according to

$$t = \frac{(M_1 - M_2)\sqrt{\frac{N_1 N_2}{N_1 + N_2}}}{\sqrt{\frac{M_1\sigma_1^2 + N_2\sigma_2^2}{N_1 + N_2 - 2}}}.$$

This quantity is then introduced into an appropriate table to evaluate its significance (Simpson and Roe 1939, p. 206). This last method is somewhat more lengthy but should be used if samples are very small or if they are only moderately large and significance is doubtful. In general, $d/\sigma_d = 3.0$ should be taken as the minimum for a significant difference.

The methods just described are perfectly valid but they ignore the fact that animals are differentiated from one another not by this or that character, but by the sum of many characters. Further, it takes no account of the ontogeny, whose importance is stressed in a section below. Quite apart from this, the method can be a source of

[2] The procedure here has been oversimplified. A more rigorous treatment, not needed here, is given immediately below.

error among those who use statistical methods without understanding them. These persons might take two samples, each consisting of a growth series, and then compare the samples *in toto* by the method above. The mean in this case is the mean size of half grown specimens, the minimum size is that of the smallest of the youngest specimens, the maximum size is that of the largest of the oldest individuals. Such a procedure is meaningless and lacking in biological significance. If there is one dictum which should be established in quantitative paleontology, it is this: Comparisons of one character to be valid *must* be made at comparable growth stages and at comparable growth stages only. If the above method is used with circumspection and with an acute consciousness of its shortcomings, it will often be useful. It has the advantage of involving only short, simple calculations which, with a calculating machine will consume but little time. In general, however, it is preferable to use one of the other methods outlined below.

It is a decided improvement to compare two characters simultaneously, particularly if one is dealing with growth series. The computations involved are more complex and longer but by no means formidable. Let the two characters in question be X and Y respectively and the two samples 1 and 2. The coefficient of correlation (r) of X and Y is first calculated,

$$r=\frac{\Sigma(d_x d_y)}{N\sigma_x\sigma_y}$$

for each sample. Next, σ_{d_b}, is calculated from one of the following equations:

$$\sigma_{d_b}=\sqrt{\frac{N_1\sigma_{Y_1}^2(1-r_1^2)+N_2\sigma_{Y_2}^2(1-r_2^2)}{N_1+N_2+4}\left(\frac{1}{N_1\sigma_{x_1}^2}+\frac{1}{N_2\sigma_{x_2}^2}\right)}$$

or

$$\sigma_{d_b}=\sqrt{\frac{\Sigma(d_{y_1}^2)(1-r_1^2)+\Sigma(d_{y_2}^2)(1-r_2^2)}{N_1+N_2+4}\left(\frac{1}{\Sigma(d_{x_1}^2)}+\frac{1}{\Sigma(d_{x_2}^2)}\right)}$$

The second equation is somewhat preferable in dealing with raw data. Next, for each sample, there is calculated the value of b_{yx} the regression coefficient, using either

$$b_{yx}=\frac{\Sigma(d_x d_y)}{\Sigma(d_y^2)} \quad \text{or} \quad b_{yx}=r\frac{\sigma_y}{\sigma_x}.$$

From these, d_b is calculated, either by $d_b=b_{yx_1}-b_{yx_2}$ or $d_b=b_{yx_2}-b_{yx_1}$, whichever gives a positive number. Then d_b is divided by σ_{d_b}, (d_b/σ_{d_b}). If the result is 3.0 or more, the two regressions, and the two samples, may be considered to differ significantly. This method takes into account the absolute sizes of the characters, their rate of development and their variation at different growth stages (see the section on ontogeny below). It is therefore much better than the preceding method.

The method of preference, however, is that of multivariate analysis which deals simultaneously with as many characters as one chooses to use. This gives the closest approach to an actual comparison of animals. Since this method seems to be entirely unknown to paleontologists, it may be well to discuss its meaning.

A point may be plotted into a line, a plane, or a "solid," depending on whether the point has one, two or three coordinants. In this case, let us use each specimen as a point and the value of each character studied as a coordinant. If we wish to compare seven characters in two samples, we, in effect, set up a seven-dimensional coordinant system and plot each specimen or point into that system. Thus each sample will be represented as a seven-dimensional cluster of points. We then study the dispersion of the points of each sample, first separately and then as a combined sample. This done, we can decide whether the two clusters (samples) are actually distinct or whether they could have been drawn as samples from a population whose variation would contain both. No higher mathematics are necessary for the calculation, only simple arithmetic. The calculation is, however, lengthy and an electrically driven calculating machine is a necessity. Slide rules *cannot* be used except possibly as a check and longhand calculations would be prohibitively time-consuming. In spite of these limitations, the fact

that this method really compares specimens rather than characters makes it the method of choice in all doubtful cases.

At this point, a few parenthetical remarks concerning the use, and misuse, of statistical methods seem advisable. Statistical analysis is admittedly in bad odor with a great many paleontologists, and for a variety of reasons. One objection, which is constantly made, is that statistical methods may be a good thing for a number of specimens, but not with only a few. There are at least two fallacies evident here. First, there are statistical methods suitable for dealing with anything from 1 to 1,000 or more specimens. Secondly, anything which a person attempts to do with a small sample, which he could not do by statistical analysis (such as unduly exact discrimination of species), will probably be founded on error. Especially, with large samples, a person not using a quantitative technique may look for and find differences between the extremes of variation of two samples and then conclude that he has been able to distinguish between samples which statistical analysis would show to be the same. Such a conclusion is entirely unjustified. One of the chief services of statistical methods in paleontology is the erection of signposts saying "Danger! Your data are no good beyond this point!" Such a guide is extremely helpful in guarding against exaggerated notions as to how much can be done with a few specimens.

Still another consideration concerns the fact that statistics have so often been misused by those who have tried to apply these methods to paleontology. This is so either because of a lack of knowledge of the purpose and limitations of the methods used or because a of lack of appreciation of the philosophy behind them. Little can be gained by citing those who have used the right method in the wrong place, but they are all too numerous in geology as a whole and not only in paleontology. Perhaps even more serious has been the use of statistical methods by those without a grasp of its philosophy. This results in the use of statistical analyses as ends in themselves, or their use from some vague realization that such analyses should be made but with only a feeble attempt to relate them to the problem at hand.

Statistical methods are, first and foremost, tools and should always be used as such. They are also sharp tools, and if misused, they will do more damage than good. Used correctly, they are a powerful aid in attacking problems not otherwise soluble. No one, however, should undertake to use statistical methods unless he has a firm grasp of their uses and applications and a thorough understanding of the philosophy involved.

HOLOTYPES AND HYPODIGMS

On the basis of what has gone before, it should be clear that the larger the two samples are, the more precise their comparison can be, and, other things being equal, the closer their means can be together and still be significantly different. Quite apart from the mathematics involved, it must be clear that the larger the sample, the more nearly we can approximate the population, and the closer we can approximate the population, the closer it can be to another equally well known group and still be distinguished from it as a separate population.

Let us suppose that we have an unknown sample which we wish to compare to a previously known species. We will then want to compare our unknown to the largest possible sample of the described species in order that our comparison may be as accurate as possible. In all too many cases, the only data available are that for the holotype. There seems to be a widely current impression that the holotype of a species is the standard of comparison for a species. It is obvious where such a concept leads. Instead of an adequate sample of the known species, such as may have been originally available, we are asked to compare our unknown to a single specimen, the holotype. We are asked to make our comparison under the worst possible conditions. In fact, the only condition which could be worse would be to have no specimen at all.

The idea of the holotype as used in this sense, plainly shows the influence of the concept of archetypes already alluded to above. As a matter of fact, the holotype is a standard for nothing except itself. "The type is typical of nothing. It is only an indication of which groups of individuals must be associated with a particular specific name. It is the final court of appeal for purposes of

nomenclature only" (Williams 1940). The holotype is merely a specimen to which the name of the species must be attached no matter what the limits of the species are. In itself it tells us neither more nor less than any other specimen. G. G. Simpson has made a very pertinent suggestion in this matter. It is that the entire collection used in the description of a species be treated rather as collective types, a hypodigm. This collection would allow the comparison of known and unknown to take place under much better conditions.

RECOGNITION OF SYNCHRONOUS SPECIES

One of the most inherently difficult problems to which a paleontologist can apply himself is involved in the recognition of synchronous species, that is, species which belong to the same genus and which were in existence at the same time. It is also a problem whose implications have been blithely ignored by a majority of paleontologists.

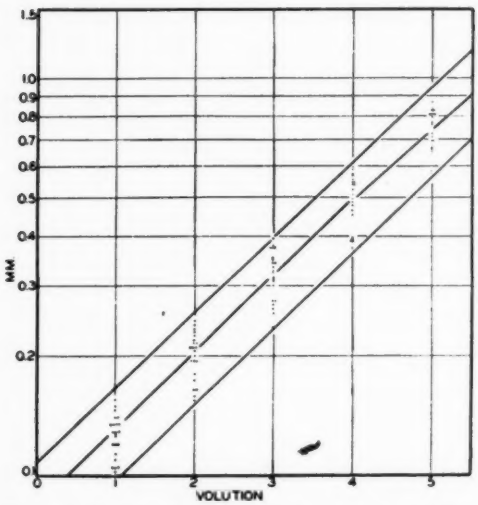


FIG. 2—Graph of radius vector plotted against volution number of a Plattsmouth limestone *Triticites*. The outer lines bounding the field of points represent the approximate limits of variation of this character. The middle line connects the mean radius vectors for each volution of the sample.

The simplest aspect of this problem entails the recognition of young and mature individuals of the same species. Only too often these have been separated and made into two or more species. There is no "Open Sesame" for handling this problem. Fortunately, the form of the young animal is often preserved in the adult, either in the early stages of a spiral shell or in growth lines on the early portion of a shell or plate. If, as is often the case, the size of fossils belonging to one genus in a collection ranges from small to large, they should be tested to see if they form a growth series as discussed below under Ontogenies. The application of common sense to the problem should result in a ready solution. It should be remembered that the proportions of a young individual may be very different from those of the mature animal. For example, the ratio of the size of the head to that of the body is much greater in a human infant than in an adult. The chief thing to remember, however, is that big animals were little when they were young and it must be expected that such young individuals will be found.

A more difficult aspect of the problem is encountered in the recognition of true species in a collection from one restricted zone and locality. We are here confronted with the phenomenon of correlation. It does not seem to have been generally appreciated that many characters of animals are correlated with one another so that when one varies, others vary also, in accordance with certain definite ratios. For example, tall men have long arms and short men have shorter arms. If the ratio of height to arm length be calculated in each case, it will be found that the two ratios are about equal, that height and arm length are connected by a rather constant ratio. This is a matter of great significance in the recognition of synchronous species.

If we take a group of mature individuals from one locality and horizon and separate them into two groups on the basis of the size of one character, we will find that we have separated them on the basis of most other characters as well. Then if we are not familiar with correlation, we may conclude that we have two species, each with a definite set of characteristics.

To consider an example, Figure 2 shows the distribution of a growth series of an undescribed fusulinid from the Plattsmouth limestone. The radius vector is plotted against the volution number. Since this is a

spiral shell, a growth series is obtained and the measurements shown for the third volution, for instance, are made on the same individuals as those for the fourth volution, and so on. The diagonal center line connects the mean radius vectors of all volutions. We now note which individuals have a radius vector greater than the mean for the fifth volution and which less. We separate these two groups to form two samples and then recalculate the means of the radius vector for each volution. These new means are then plotted and connected by a line (fig. 3). The means of the radius vectors of each sample are now well separated over the whole area of the graph. If we now calculate the means of the height of volution and septal count for the same two samples and plot them (fig. 3 also), we find that these means are also separated by the same process, and in the same direction. The differences between these means are as great as are commonly used to distinguish between fusulinid species. We have, then, created two "species" where one grew before, and neither has any validity or reason for existence.

Here again there is no clear-cut method to avoid error. As was pointed out above, it seems best in the long run to proceed on the preliminary assumption that only one species of any genus will be present at any one locality and horizon until good evidence to the contrary is apparent. The preceding paragraph should make it clear that an unthinking attempt to split up a group of individuals will probably be successful—and probably be wrong. If it is suspected that a group of individuals is not homogeneous (represents more than one species) probably the best way to work is with a pair of characters. If we can split our group into two well-defined parts, one of which has the

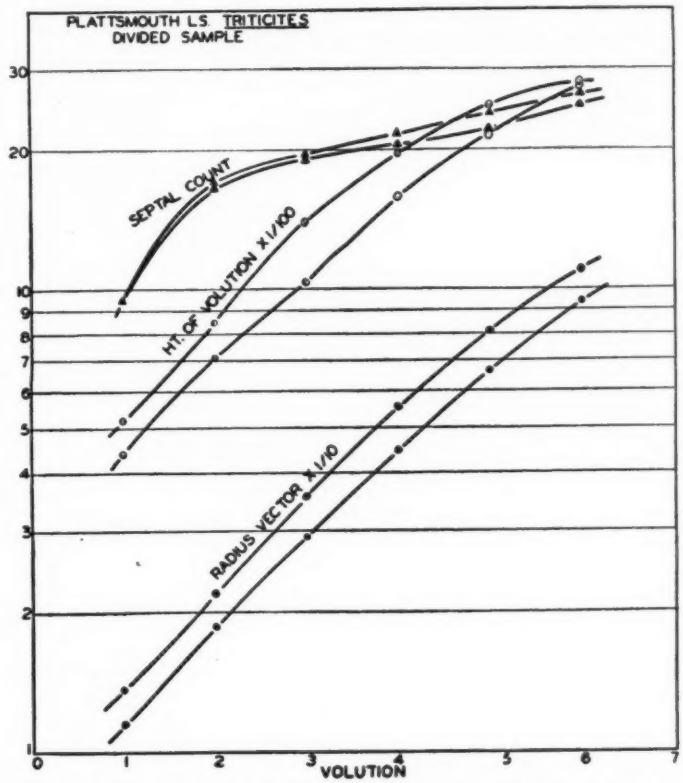


FIG. 3—Graphs showing the means of the divided sample of Plattsmouth *Triticites*, as explained in text. Radius vector and height of volution are measured in millimeters.

ratio of character A to B of, say, 1:2 and the other part having the same ratio as 1:4, then we are on firmer ground in recognizing two species. In this situation, we are, in effect, working against correlation. This procedure is by no means free from criticism and each case must be examined solely on its own merits. In general, single characters of size, counts, and simple angular relations are the poorest, and indeed, for the most part unusable in splitting a sample. Shape and form characters depending on a combination of simple characters are more successful but still cannot be used blindly since a form character which seems to depend on the interaction of several simple characters, may actually be found to be chiefly the result of a single size character. From all this it should be clear that the recognition of synchronous species is among the most difficult and uncertain tasks to which the paleontologist can apply himself.

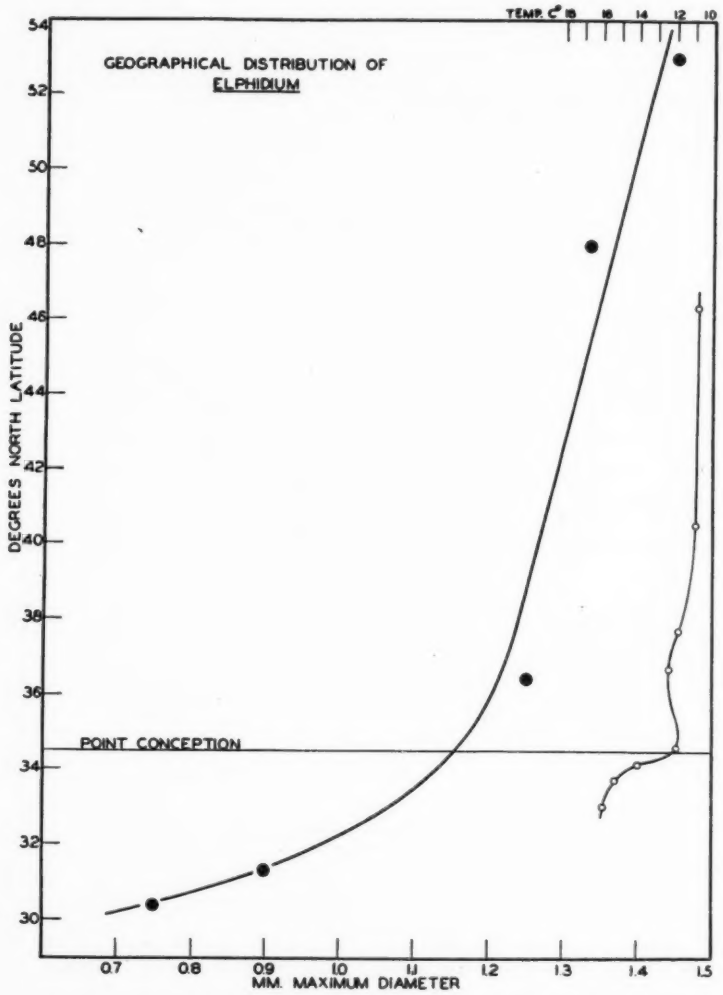
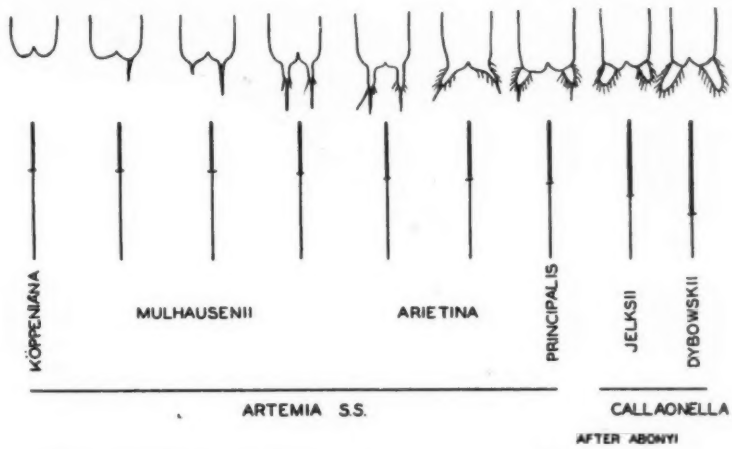


FIG. 4—Geographical distribution of *Elphidium "crispum"* on the Pacific coast. The left hand curve shows the maximum diameter plotted against the latitude. The right hand curve shows the corresponding coastal water temperatures.

CLINES

In the preceding section we considered the problem of recognizing species within a population existing at one place and time. Numerous other factors enter in if the population, still of one time, is spread over an area of notable extent. In addition to the question of "Are the differences statistically significant?", we must face the question of "Are the differences genetically significant?". To illustrate some of the difficulties involved we may use the data presented by David Lower California, Lat. 30° 25′N. Nicol measured 200 specimens each of the subspecies of *E. fax* and a 200-specimen sample of *E. excubitor* and *E. concinnum* combined. These data were analyzed and, from the results, he concluded that these are valid species and subspecies which are characterized by statistically significant differences.

If we examine these data, we find that, from north to south (fig. 4), the maximum diameter of the shells decreases with notable regularity. Similarly, but less regularly, the



BRINE-SHRIMPS FROM MORE OR LESS SALINE WATERS.
UPPER FIGURES: TAIL SEGMENTS AND FINS.
LOWER FIGURES: RELATIVE LENGTH OF CEPHALOTHORAX AND ABDOMEN.

FIG. 5—Variation in the brine shrimp.

Nicol in his recent paper on West American species of the genus *Elphidium* (Nicol, 1944).

In this paper Nicol presented a study of what has been called *Elphidium crispum* on the Pacific coast of North America, and recognized in its stead *E. fax fax* and *E. fax pingue* from the Recent, *E. fax barbarense* from the Pleistocene, and *E. excubitor* and *E. concinnum* from the Recent. We shall not concern ourselves with the Pleistocene form here. Of the rest, *E. fax fax* comes from the Straits of Juan de Fuca, Washington, Lat. 48° N; *E. fax pingue* from Monterey Bay, California, Lat. 36° 37′ N.; *E. excubitor* from Punta Penasco, Mexico on the Gulf of Lower California, Lat. 31° 21′ N. and *E. concinnum* from San Quentin on the Pacific side of

thickness, number of chambers in the last whorl, and the number of retral processes on the last chamber decrease with decreasing latitude (and, in general, increasing water temperature.)

This notable regularity of decrease of size with increasing temperature may lead us to wonder if we are here faced with a genetic difference, or one in which the primary control is environmental. To illustrate the reasonableness of this last supposition, let us turn aside for a moment.

The brine shrimps are small crustaceans, world-wide in distribution. They are found in saline waters ranging from almost fresh to those so concentrated that salts are precipitating. Early students noted a great

variation in the form of these animals from place to place but a relatively constant form in any particular occurrence. As shown in fig. 5, the character of the distal end of the abdomen and the ratio of length of cephalothorax to abdomen are extremely variable, and almost every other external character is equally so. On the basis of these combinations of variations, the brine shrimps illustrated were placed in four species of *Artemia* in suitable environments, developed into over thirty "species" of the genus (Scott, 1924).

If this be true, and to such an extent, in animals of as high a degree of organization as arthropods and molluscs, it should not be surprising to find similar effects in protozoans.

In returning to Nicol's data, it is necessary first to examine his statistical conclusions.

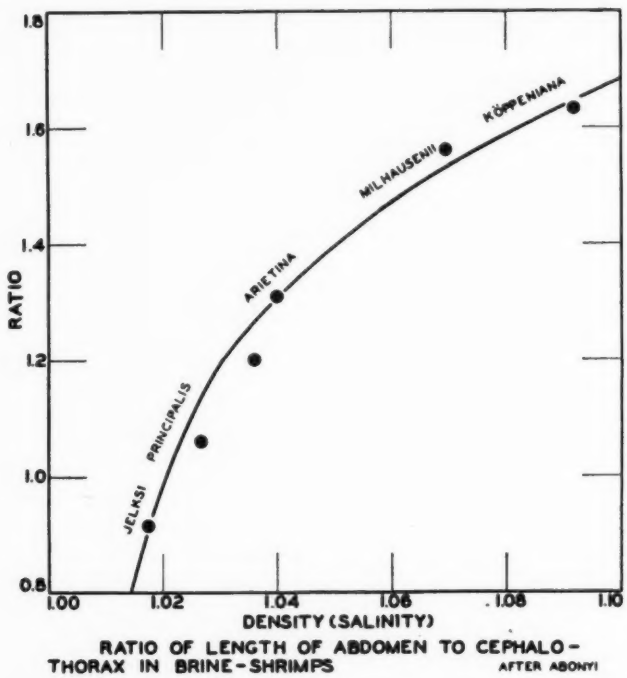


FIG. 6—Abdomen to cephalothorax ratio of brine shrimps plotted against the salinity of the water in which they are found. Note how closely the points come to falling on a smooth curve. The forms with the largest and most hirsute tail-fans occur in the freshest water where buoyancy is most needed.

and two of *Callaonella* as shown. Unfortunately, it was then found that if the eggs of the brackish water *C. dybowskii* were reared in extremely saline water, *A. koppeniani* developed from them. It soon became clear that the six forms were one genetic group (species) of the same genetic constitution (genotype) whose external form (phenotype) depended on the environment in which it found itself (fig. 6). Similarly, eggs from a single individual of the pelecypod genus *Anomia*, have, on being hatched and reared

Though giving all due praise to Nicol for placing his study on a quantitative basis, we must conclude that the methods he chose to use in the analysis of his data were most unfortunate. Since the reasoning involved in these choices has been followed by others, it seems worth while to examine it further.

In his study Nicol used regression diagrams and by plotting one character against another derived "ontogenies." However, instead of using these growth curves for

comparisons, he used maximum diameters. "Maximum size was used rather than mean size because the smallest specimens were not available. Small shells of young individuals are more fragile and easily destroyed by waves and predatory animals. Without the smaller sizes, the location of the mean would naturally be affected. The maximum size, therefore, was the only stable measure that could be used in comparing species or communities within a species" (Nicol, 1944: p. 179). There are several serious misconceptions in these sentences. The central one concerns the idea of the mean size of a species. As Nicol uses the word "mean," it becomes the average size between that of the oldest and youngest specimens (see above, One or Two Species?). If, using this idea, we measure a random sample of the human male population, we would find that height varies from about 18 inches for infants to about 78 inches for large adults, and that the mean height of human males is about 48 inches, an obvious absurdity. The mean size of a growth series is not a point, but a line. There is no single mean size for an animal; there is a mean size for each growth stage. This is a point which Nicol, and certain others, have missed entirely and it brings down their whole analysis. The fact that the youngest members of a population are not available is certainly no reason for turning one's back on all but the largest. Furthermore, as has already been pointed out it is much more preferable and accurate to compare regression lines for two characters than it is to compare single characters. The maximum size, subject as it is to variations due to sampling (all extremes being more uncommon) is certainly not "the only stable character that can be used for comparing species." Rather, it comes nearer to being the most unstable. Nicol's estimates of significance, given on his pages 180 and 181, must therefore be rejected as being based on an erroneous supposition. These comments also apply with lessened force to his estimate of significance of ratios, though I agree with his conclusion that "Most of the ratios are not significantly different."

If, instead of using these unsuitable methods, we test for the significance of the differences of the regression lines, we come to quite different conclusions. In the case of *E. fax fax* and *E. fax pingue*: comparing the regression lines of the greater on the lesser diameters for both subspecies, $P = 0.70$ (Nicol's value, $P = 0.0001$ for both subspecies and both characters). Other characters give similar results. In other words, based on these two characters, the probability is 70 in 100 that the two samples do not differ significantly, that the differences observed could be due to sampling errors. On such a basis, there seems to be little reason for recognizing the two subspecies and we are left with simply *E. fax*.[3] On the other hand, if we compare *E. excubitor* and *E. concinnum* taken together (data for the two are not separated in Nicol's paper) with *E. fax* for the significance of the difference of the same two regression lines, we find that $P = 0.0008$ (Nicol's values, $P = 0.0001$). This figure is decidedly significant, though rather less so than Nicol's calculations would indicate. Data are not presented which will allow us to decide whether *E. concinnum* differs significantly from *E. excubitor*, but on the basis of what is given, it would not be surprising if it did.

The question remains as to the meaning to be ascribed to the fact that *E. fax* and *E. concinnum* are statistically different. Nicol and others seem to proceed on the *a priori* assumption that a statistical difference necessarily means a real genetic difference. In the brine shrimps and in *Anomia*, however, greater differences are without genetic significance. If we examine the geographic distribution of these forms of *Elphidium*, we get a suggestion that the situation is similar to that of the brine shrimps and *Anomia*. As Nicol pointed out, there is a "break in the distribution of *E. "crispum"* just north and south of Point Conception." If we examine the water temperature of the area, shown on the right side of fig. 4, we see that this break corresponds almost exactly to a sharp drop in the temperature of the coastal waters of the same area. In view of the general correlation between size and other characters, and water temperature, as already noted, it does not seem likely that this is mere coincidence.

[3] Both the above and what follows have been written solely as an illustration of principles. Under no circumstances is it to be viewed as a revision of the nomenclature of *Elphidium*.

On the basis of the above factors, it would seem reasonable to conclude that the west coast Elphidiums of the *crispum* group are a genetic unit, and that their division into species is not warranted; that the variation found is a result of differences in water temperature which controls the form of the phenotype of a single unit. Such a unit fits in well with the definition of a cline (Huxley, 1939), a population which varies progressively from one end of its range to the other. In this particular case, it seems likely that the variational control is primarily environmental rather than genetic. Strictly speaking, there seems little reason for attaching names such as *fax* or *concinnum* to non-genetic variants, whether such variants be considered as species, subspecies or varieties, and one name should be applied to the whole unit. Other, practical matters, however, enter into this problem which demand a consideration of infraspecific units before a decision can be reached in this case.

INFRASPECIFIC UNITS

If it is difficult for paleontologists to agree as to what a species is, it is even more difficult to get any agreement on the vexed problem of infraspecific units. There are three kinds in more or less regular use in paleontologic literature. One is based upon geographical variants of a species, another upon time variants and the third upon morphological variants at one locality. In addition, each of these may be subdivided into those in which genetic control is dominant and those in which environmental influences are more important. This makes a total of six infraspecific categories which might receive names. Paleontologists have two names for them, subspecies and variety, both having been used in various ways and interchangeably.

The International Rules recognize only sub-species, but they studiously, and perhaps properly, avoid definition of such a unit. Neozoologists, in general, use "subspecies" for geographic variants whose differences are presumably genetic. Unless paleontologists ignore the other categories, they might call all six of them "subspecies," even if this is not desirable. Also it is doubtful how many of these types of variation paleontologists can recognize.

Geographic variants. As shown above, there is a minimum range of variation of the mean ($M \pm 3\sqrt{2\sigma_M^2}$) within which we can not validly differentiate between samples. Thus if the mean of a character of sample A is found to range from 15 to 20 mm. the mean of another sample, B, should lie outside this range if we are to conclude that sample B differs significantly from sample A.

A unit so differentiated has been termed a species above. If we recognize subspecies, their means would fall within the range of the mean of the species and the differentiation of subspecies would not be statistically valid. (It is assumed in the preceding statements that the sample for the species is a composite over its geographic range.) The only alternative is to extend the limits of the species so that units defined as above would be considered subspecies. Another factor complicates the situation. So far we have assumed that we are dealing with synchronous populations (or a synchronous population). Generally, however, we cannot be sure that we have *exact* time equivalents in geology, particularly if notable distances are involved. With rare exceptions, such certainty does not exist, even to within a few thousand years. This means that in most cases, time and geographic variants are difficult to separate.

Environmental effects add to the difficulty. In modern faunas, environmental variants may be studied by breeding or other experiments as with the brine shrimps. Obviously, however, one cannot breed ammonites or fusulinids, but the problem is no less real. If such variants are suspected among fossils, one must search the environment for some parallel change. Nothing has yet been done along these lines except in the grossest manner. The difficulties are, of course, numerous. Many environmental factors left no known impress on the accompanying sediments. (It may be that this is mostly a matter of ignorance; if so, the fundamental research is yet to be done.) Diagenetic changes altered the composition and texture of sediments, and post-diagenetic changes may have changed them further almost beyond recognition. In the face of a problem so appallingly intricate it is small wonder that estimates of depositional environments have been qualitative.

Time variants. Many paleontologists have attempted to define subspecies as time variants. Evolutionary changes should, of course, show themselves in a succession of descendant populations. We are faced here, however, with the difficulty of distinguishing environmental and genetic variations and it is not likely that much can be done to separate them. In dealing with synchronous specimens there is some possibility that certain environmental influences can be recognized. In time series, it may be expected that genetic and accompanying phenotypic changes will have occurred even in a "constant" environment. If the environment changed we may expect that organisms evolved to adapt themselves to the changed environment. The difficulty in distinguishing phenotypic changes, produced by a change in the genotype, from phenotypic changes unaccompanied by genotypic change introduces much uncertainty.

Morphologic variants in local populations. Many paleontologists have dealt with individual variants as though they are infraspecific units. Genetically various though the individuals of a population may be, modern neozoologists are very hesitant about recognizing more than one infraspecific unit at any particular place. This is easily understandable. Since a species is an actually or potentially interbreeding population, the subdivisions also will be. If two morphologically distinct subdivisions of this sort come in contact it is to be expected that interbreeding would soon reduce them to a single unit. Thus a local interbreeding population will, in the aggregate, be genetically homogeneous, isolation or some such factor being necessary to develop subspecific or specific differences.

It is true that even minute environmental variations, particularly size variations, are very important in local populations. It is such variations that many paleontologists have termed subspecies and varieties.

Summary of infraspecific units. Certain conclusions may be drawn from the above considerations. First, there seems to be little reason to distinguish variants within a synchronous sample from one locality. Such variants are probably genetically homogeneous and there is no theoretical reason for a subdivision. Subdivisions based on sizes or counts are especially illlusory as they can be adequately accounted for on the basis of variations in environment, amount of food, etc. The only result of recognizing subspecies under such circumstances is to burden the literature and no useful purpose is served.

There seems to be little value in recognizing time variants in units smaller than species. Probably we are dealing with evolutionary series and there is a minimum size to significant units into which they can be split. The size of these units has nothing to do with the label attached to them, whether it be species or subspecies and it seems most useful to consider the minimum unit a species. If someone chooses to term it a subspecies, this can hardly be designated an error, but there seems little reason for such a course.

On the other hand, the subspecies is a useful unit for distinguishing synchronous geographic variants. When such variation is recognized, the entire series can be considered a species and the validly recognizable subdivisions termed subspecies. Such variation may be primarily either genetic or environmental. In fossil material it may not be possible to distinguish these influences but in some cases the evidence may point more strongly to one than to the other. If the control is genetic, the geographic variants should be termed subspecies, as they would be by the neozoologist. If environmental control is primary, the significance is not the same, but because of uncertainty it seems best to term such units subspecies also.

In the case of the West Coast Elphidiums, it would seem best to consider Nicol's valid subdivisions as subspecies. If the entire group is specifically distinct it could be termed *E. fax* with the subspecies *fax*, *concinnum*, and perhaps *excubitor*.

ONTOGENY AND HETEROGONY

A feature noticeable in most paleontological literature is the lack of attention paid to a *quantitative* study of growth stages. Many persons have ignored them as though they did not exist. Consequently, little regard has been paid to sizes when comparisons were made between samples. If the various parts of an animal maintained a

uniform ratio with respect to each other during growth, this might not be so important, but generally the proportion between any two characters changes constantly during growth. For example, if the ratio of the length of the deltoid plate to the total height of *Pentremites pyriformis* is plotted against time,[4] we get the graph shown in figure 7. In the youngest stage the deltoid is a little more than 0.1 of the height. As the blastoid grew the deltoid increased in size proportionately faster than the height and eventually reached a proportion of about 0.3 of the total height. In the final growth stages, however, the height increased at a somewhat greater rate so that the ratio falls to nearly 0.25. Consequently it is impossible to specify a certain deltoid to height ratio as a character distinguishing *P. pyriformis*. Neither can the size of the deltoid, nor the height, be used without qualification since both changed constantly during growth. Most invertebrates do not have a terminal size, as do many of the higher vertebrates (mammals); instead their parts continued growing throughout life but not necessarily at the same rate. Also the size attained by these animals at any given age is not constant.

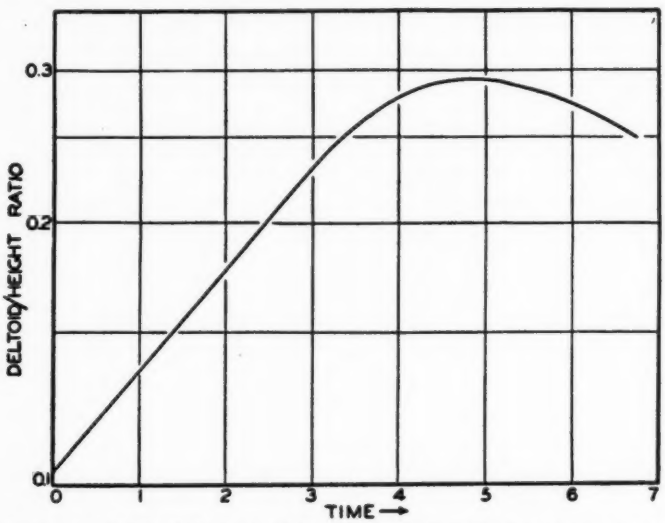


FIG. 7—Graph showing the deltoid to height ratio of *Pentremites pyriformis* as plotted against a "time" character (the standard radial).

[4] The plot is actually against the logarithm of the standard radial as is explained below.

Authors, in trying to escape these difficulties (too often dimly realized), have commonly used what they called "mature specimens" in setting up standards for a species. This is a comfortably vague term, but it is a qualitative term covering a good part of the life span of most animals and it is quite unsuited to precise work. Some authors, including the present one, have attempted to meet this problem by constructing "ontogenetic" curves for various characters and then specifying the size of the character at some particular growth stage. From what has gone before it should be clear that it is absolutely necessary so to specify the size of any character. However, so far as I know, no analysis of the method of doing this has yet been presented.

Ontogeny may be defined as the history of the development of an individual organism or of the individuals of a contemporary group. An ontogenetic curve is a graph showing this development visually in quantitative terms. In practice, of course, both are considered in terms of the development of individual characters. In either case, the essential feature of the whole idea is the change of a character or characters in terms of *time*. We can, for example, measure the height of a number of human males at birth and on their subsequent birthdays, and then

construct a curve showing the relationship between time and height in human males. This would be a truly ontogenetic curve.

On the other hand, if we deal with fossil material, no such time scale is available. We have the hard parts of animals which died at different ages (stages of development). We know that, in general, size is directly correlated with age, but because of normal variation, a younger animal may be notably larger than an older one. (The influence of sexual dimorphism will not be treated here. In most of the usable fossil invertebrates it does not seem to be very important.) With these factors in mind, note how ontogenies of fossil animals have been reconstructed. In every case, one size, or count, or angular relationship is plotted against another such character. Thus we are not dealing with true ontogenies which are plotted against time, and also our curves may not even be an accurate secondary plot against time. We have, in fact, constructed curves of heterogony showing the relative development of two characters.

These considerations are illustrated by the following example. Suppose we have four specimens with the following characteristics:

Specimen	Length	Height	Relative Age
1	2	2	2
2	3	4	3
3	4	6	2
4	5	8	3

If height is plotted against length, as might be done in constructing the usual "ontogeny," we obtain the lower line shown in figure 8. If the relative ages are as indicated above, as they well might be, the upper line more nearly represents the true ontogeny. The trends of these two lines are quite different.

Another factor may be considered in relation to the actual case of *Pentremites pyriformis* illustrated in figure 7. It might be assumed that, on the basis mentioned in footnote 4, each division of the horizontal scale represents an equal amount of time and that there is a direct, uniform (in this case exponential) relationship between the length of the standard radial and time. Instead, let us suppose that the length of the standard radial is negatively accelerated with respect to time; that is, that each successive division of the horizontal scale of figure 7 represents less time than the one preceding it. If so and if the graph be adjusted to give a uniform time scale, the

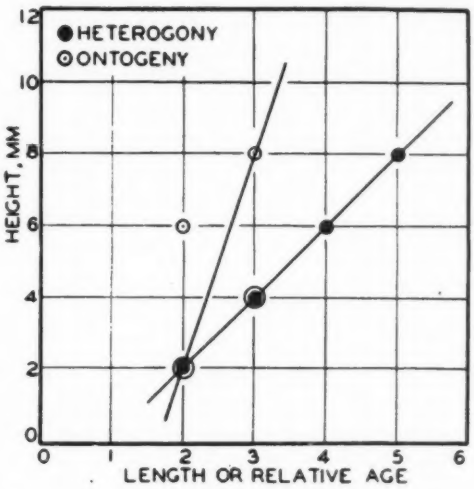


FIG. 8—Theoretical graph showing a possible relationship between ontogeny and heterogony in a series of individuals.

"ontogeny" would appear as in figure 9. Similarly figure 10 is a graph showing growth if the latter were positively accelerated. Figure 9 suggests that the deltoid to height ratio increased rather uniformly and at a rather moderate rate throughout most of the life of the animal with a slight reversal in the oldest individuals. Figure 10, on the other hand, suggests that this ratio increased very rapidly in the early growth stages and then remained more or less uniform throughout about two-thirds of the life of the animals. These are very different interpretations of the development of these characters, but there is no *a priori* reason why either of them, or neither, is a true representation.

There seems to be a possibility, however, of approximating the relative age of specimens in a growth series even though it is impossible to determine their absolute ages. In figure 11 two characters, X and Y, are plotted against one another. A least square curve drawn through these points would

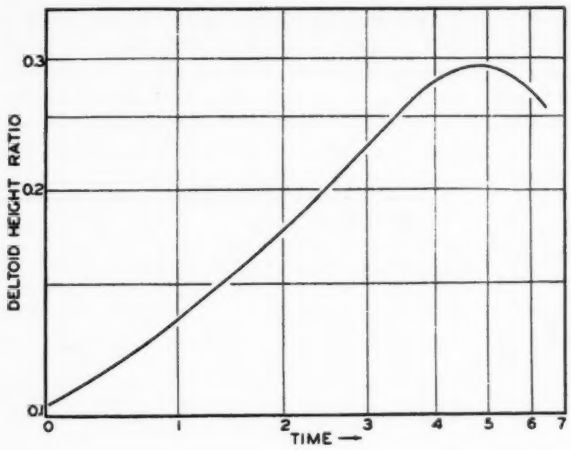


FIG. 9—Deltoid-height ratio of *Pentremites pyriformis* plotted against a progressively decreasing time scale.

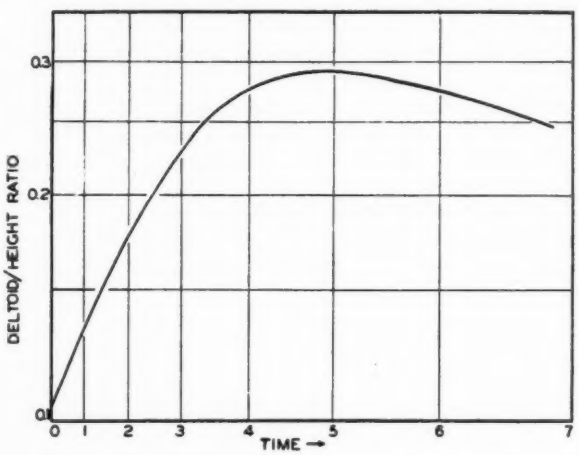
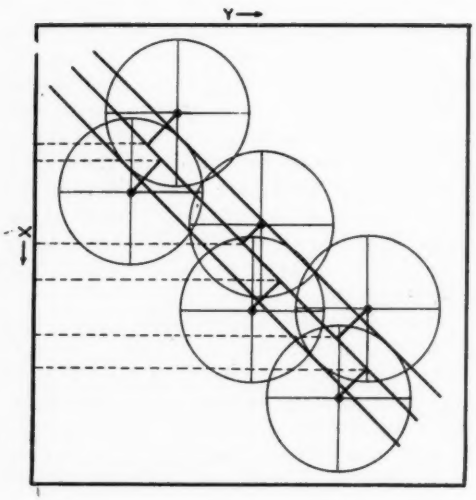


FIG. 10—Deltoid-height ratio of *Pentremites pyriformis* plotted against a progressively expanding time scale.



commonly be considered an ontogenetic curve, but of course neither character is actually plotted against time. If, however, Y were plotted against time and a true ontogenetic curve drawn, each point would lie within a certain vertical distance of the curve, this distance being determined by the inherent variability of character Y at any particular age. If we knew the standard deviation of Y from this curve, and drew through each point a vertical line of length equal to $Y \pm 3\sigma$, the ontogenetic curve would pass through all the vertical lines at one place or another ($P = 0.997$). Character

FIG. 11—Diagram illustrating the method of approximating the relative ages of specimens in which the heterogony of two characters is known.

X may be treated similarly with horizontal lines. If, for either character, we draw a curve as high as possible which cuts all the lines, and similarly one as low as possible, we can draw circles of a radius 3σ instead of horizontal and vertical lines. A moment's consideration will show that the length of the radius is of secondary importance so long

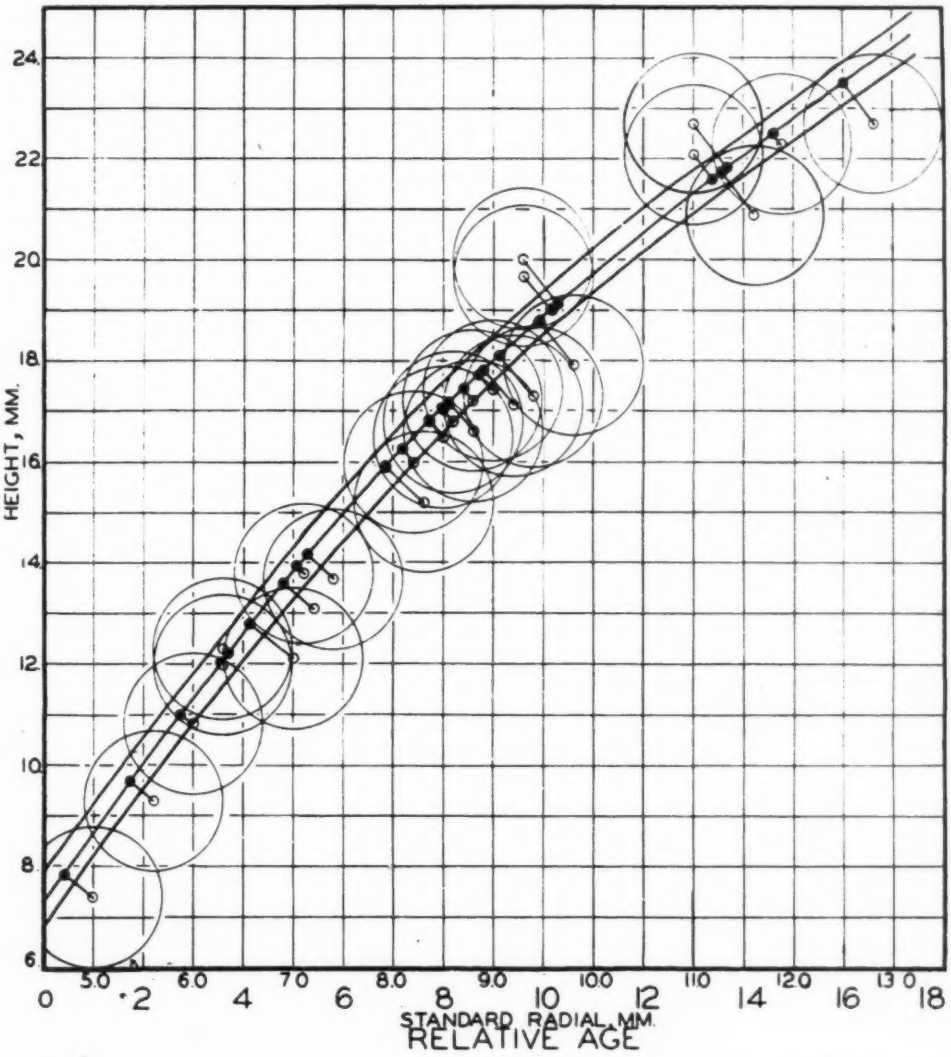


FIG. *12*—Graph showing the estimation of the relative age of individuals in a sample of *Pentremites pyriformis*.

we would know that the true ontogenetic curve must lie on or between them and most probable place for it to occur would be midway between them. If, instead of plotting X and Y against time, we plot them against one another and apply the same reasoning, as it is uniform and long enough to allow a line or simple curve to cut all the circles. If the radii are needlessly large, the two bounding curves will be far apart, but uniform with respect to the midline. If we construct suitable circles as in figure 11, and

proceed as above a midline curve is obtained expressing a relationship of X and Y to time. If we now drop perpendiculars from the plotted points to this curve, the intersections of these lines and the curve will be the most probable positions from which each specimen varied in X and Y. These are points in time and their relative positions on the curve indicate the relative ages of the specimens. Finally, if we project these points onto an arbitrary scale on the X-axis, we can read off the probable relative age of each specimen studied.

An actual example is shown in figure 12, where height of the blastoid *Pentremites pyriformis* is plotted against the length of the standard radial. (These terms are defined below in the section on blastoids.) These two characters were selected because they show closer correlation than others and would probably give the best results. The circles drawn around the points have a radius arbitrarily chosen but probably approximating 3σ. The original data indicate that the regression line is slightly curved and allowance was made for this in drawing the two outside curves, one as far to the upper left as possible, and still touching all circles, and the other as low as possible to the right. The time curve is midway between these and the original points were projected onto it. These final points may in turn be pro-

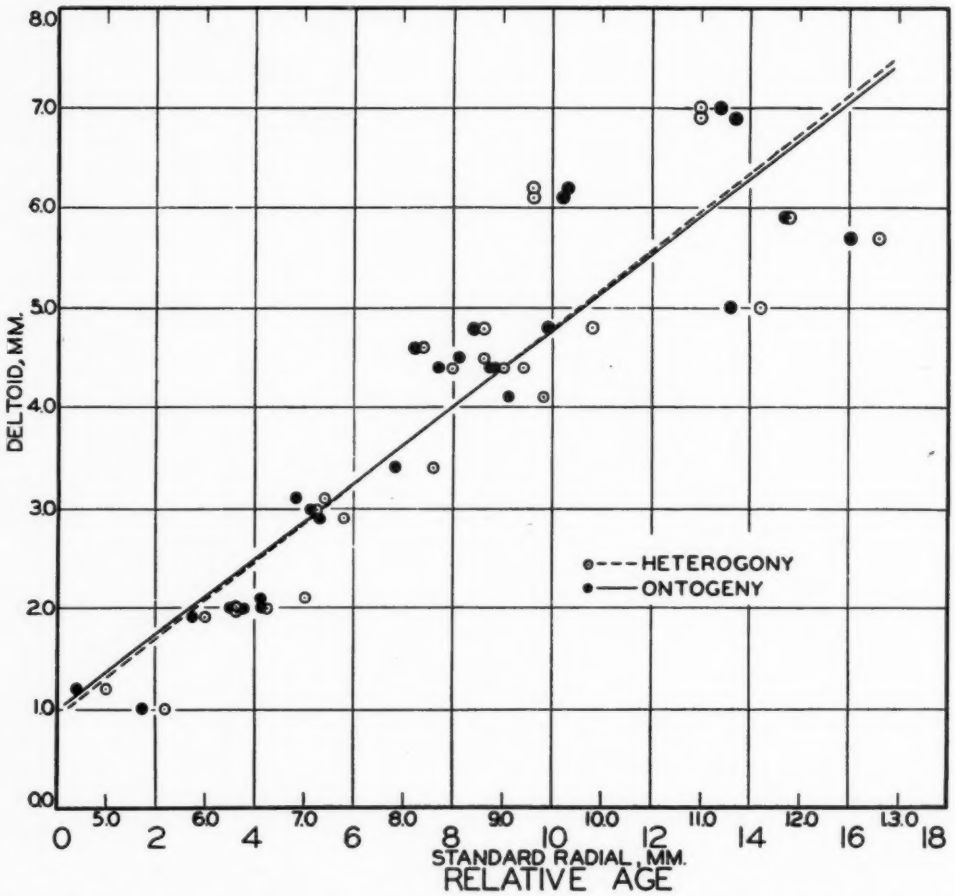


FIG. *13*—Dispersion of points representing the height of *Pentremites pyriformis* plotted against the standard length compared to the dispersion resulting from plotting height against relative age.

jected onto an arbitrary time scale along the X-axis.

Of course such a procedure can lay no claim to great accuracy. If we were to use a different pair of characters, we would arrive at a somewhat, though not widely, different set of relative ages. Also there may be a multiplying or exponential factor involved which, although not affecting the age-order of the specimens, might greatly affect their spacing.

With these reservations recognized, the effect of plotting some character against relative ages may be compared with plotting the same character against another. In figure 13 the length of the deltoid of *P. pyriformis* is plotted against the relative ages (points shown by solid circles) and also, on a precisely comparable scale, against the standard radial (points shown by open circles). The points plotted against relative age have somewhat less scatter than the others, as might be expected. Whether or not this is advantageous may be determined by considering the regression lines for the two sets of data.

By the usual methods the regression lines are calculated as follows: Deltoid $=0.38$ (Relative age) $-$ 1.0 and Deltoid $=0.77$ (Standard radial) $-$ 2.5. These two lines, shown in figure 13 (Deltoid against relative age, continuous line; deltoid against standard radial, dashed line), almost coincide and are so similar that there is no need to compare them statistically. Evidently plotting this character against time has not changed the trend of the resulting curve, and, conversely, it makes little difference whether this character be plotted against time or another character so far as the trend of the regression line is concerned.

Next, the deviations from its regression line are calculated for each set of points, and from this the standard deviations are obtained. For deltoid against relative age, $\sigma=0.69$ mm., for deltoid against standard radial, $\sigma=0.76$ mm. These standard deviations also indicate that the first set of points has somewhat less scatter than the second. However, if the two are compared, we find that $d/\sigma_d=0.5$ which is decidedly not significant ($P=0.38$). ($d/\sigma_d=\sigma_1-\sigma_2/\sqrt{\sigma_{\sigma_1}^2+\sigma_{\sigma_2}^2}$ samples are of the same size.) Thus, plotting of deltoid against time (or a time factor) has not significantly improved the scatter or, conversely, it makes little difference in the scatter whether the deltoid is plotted against time or another character.

Other examples could be cited to show the same relations, but this would be merely repetitious. The conclusion to be drawn is that, under certain conditions, we are justified in using curves of heterogony as ontogenetic curves as they probably are not greatly in error. The conditions alluded to need some explanation,

If the necessity for the use of growth series in paleontology be granted, it is desirable for them to be as uniform as possible within any particular group of fossils. Therefore it is necessary to select one character to be used throughout the group as a "time" character. For example, in the section on blastoids, the selected character is the "standard radial." All other blastoid characters are then studied in relation to this one. This "time" character should have certain attributes. It should be present and measureable in all growth stages; it should change slowly and uniformly and measurably during growth; it should, insofar as possible, be free from gerontic effects; it should be present in a usable fashion in all members of the group; it should not be subject to drastic modification in any species. It may not be possible to satisfy all these requirements fully, but every effort should be made to do so.

PRESENTATION OF DATA

Thus far emphasis has been placed on the theoretical aspects of quantitative paleontology. If the application of these methods to actual fossil material is attempted, a variety of problems arise, one of the foremost of which is the problem of deciding on the most suitable way to organize and present quantitative data. The following discussion is devoted to the general principles involved. Actual examples of application of the methods here discussed are presented in the succeeding sections.

Little difficulty is encountered in the presentation of the data of qualitative paleontology. One simply describes in words what he considers to be the important features of the fossil in question, and perhaps supplements this description by meas-

urements of a few specimens.

If, instead, the study is to be quantitative, we are confronted by a mass of raw data both ponderous and indigestible. Our first concern is to reduce this mass of data to manageable and comprehensible proportions. This can be done partly by graphical and partly by mathematical means. The original raw data should in all cases be presented, however. This allows others to check the author's conclusions with an exactness and fairness not otherwise possible.

There are, essentially, three things we wish to know about any character: its size, its variability, and its relations to other characters. The size of a character cannot, of course, be given by any single number. It varies during growth in any individual and, at any particular growth stage, it varies between different individuals. The usual, and probably the best, way of dealing with this situation is to report the mean or average size. This is a measure which must be qualified. If the specimens dealt with are of essentially similar age, a simple situation but one to be avoided, the mean will give a logical measure of the central members of a population. However, if more than one growth stage is present in the sample, the mean is a biologically meaningless measure. This may be illustrated by a theoretical example. Suppose that we have a series of ten specimens whose respective lengths are 1, 2, 3, 4, 5, 6, 7, 8, 9, and 10 cm. It should be apparent that we are dealing with a growth series. If we calculate the mean of this series ($\Sigma(X)/N$), we obtain the figure 5.5 cm. which has practically no significance. It has precisely the same meaning as the statement that the average height of human males is that of a nine year old boy because his height becomes midway between that of an infant and an adult. It is necessary, therefore, to specify the average size of each growth stage. Since there is an infinity of growth stages for any species, we should have to specify an infinity of averages. The simple way of handling this situation is to give the equation of the line which passes through the successive averages. This is the regression line which should be used without exception in all cases involving growth series. Although a curved regression line may sometimes fit the data better, the equation for a straight-line regression should always be used, because there is no simple method for comparing two curved regression lines in a test for significance. As a convention, the regression should always be expressed as one of the dependent on the independent variable (Y on X).

The variability of a character is most simply stated in terms of the standard deviation. In a sample involving substantially one growth stage, this measure can be calculated from the deviations of the observed readings from the mean. In the case of growth series, however, the standard deviation *must* be calculated from deviations from the regression line in order to be meaningful. It can readily be observed that the *absolute* amount of the deviation from the regression line is less in the early than in the late growth stages but that the percentage or *relative* deviation remains much more constant. The standard deviation from the regression line should actually vary continuously during growth, being least in the youngest stages and, thereafter, steadily increasing. If the standard deviation be calculated as suggested above, we obtain not a variable but a single standard deviation. A moment's consideration will, however, show that we have, essentially, obtained the standard deviation of the latest growth stages where the absolute variability is the greatest. Of course, the total effect is to reduce the emphasis on the amount of scatter since the lesser scatter of the early stages is "averaged" in with the greater scatter of the later stages. It is believed, however, that a larger sample, consisting of all growth stages leads to better results in most cases than a smaller sample available for any single growth stage. One can plot the regression line on a logarithmic or semi-logarithmic graph and mark off the standard deviation at its upper end either above or below the regression line. A line is then drawn through this point and parallel to the regression line. The difference between these two lines at any particular growth stage will then give a usable value of the standard deviation for that stage.

The relations between characters may be shown by ratios, the usual way, or by plotting one character against another. In either case, the data are best presented

graphically. A table of numerical figures does not in itself mean very much but if presented graphically, measurements can be comprehended at a glance.

These last considerations raise the question of the most suitable manner in which data may be presented graphically. The most generally usable type of graph is the line graph. Such types as the pie graph, bar graph, etc., may sometimes be useful but they have no such general application. However, a line graph may be constructed in a number of different ways. The most common type of line graph is arithmetic in which the coordinates are spaced at equal intervals. This type is widely used but is not necessarily the best for biological data, particularly those involving growth series. Most ontogenetic curves are found to conform more or less well to a curve of the type $Y=a+bX^k$. If this type of curve be plotted on an arithmetic scale, it will often be found to rise with undue steepness in the later growth stages, a familiar property of exponential curves. Further, the absolute variation is so much greater in the later than in the early growth stages that, relatively, the amount of variation shown by older specimens is overemphasized and that of the younger specimens underemphasized. If, however, this curve is plotted on a logarithmic scale, it will usually be found to approach a straight line. Those which are curved on a logarithmic plot are affected by a number of factors not particularly pertinent to the present discussion, but they are more manageable than those resulting from arithmetic plots. The variability is nearly constant on a logarithmic plot; that is, the lines containing the variability are almost parallel rather than widely divergent as in arithmetic plots. The total effect is that the young and the old stages are given equal weight on the graph which is surely desirable.

In some cases, the dependent variable may be plotted against the whorl or volution number, as in cephalopods or fusulinids. In such fossils, the spiral formed by the shell is a logarithmic (exponential) function and thus the successive whorl numbers will be spaced logarithmically. In these cases, the graph should be semilogarithmic, the dependent variable being plotted on the logarithmic and the independent variable (whorl number) on the arithmetic scale.

In some instances, triangular graphs may be used to good advantage. These are discussed below in connection with specific problems.

PRACTICAL APPLICATIONS OF QUANTITATIVE METHODS

The remainder of this paper is devoted primarily to applications of the methods explained above. In addition, certain developments and consequences of the theoretical considerations are brought out. Five types of animals are discussed: the blastoids typifying those whose skeletons are made up of separate plates, the pelecypods and the brachiopods typifying those which have two valves, the gastropods typifying those whose shell is spiral and whose protoconch is usually not preserved, and the fusulinids whose shell is spiral with an internal protoconch (proloculum). The great majority of fossil invertebrates fall into one or another of these shell types.

Blastoids

The material used for this study consists of a collection of *Pentremites* from the Paint Creek formation of Chester age, collected from an outcrop 1½ miles west of Floraville, Illinois. One part of this collection consists of the characteristic and easily separable *P. pyriformis*. Data concerning this form have been used above. The rest of the sample consists of specimens usually referred to *P. godoni*.

The study of blastoids has been almost entirely qualitative. The first problem in this study, therefore, was the setting up of a standard system of measurements. The one selected is suitable to the forms studied but it might have to be modified slightly for other genera.

The blastoids are invertebrates whose skeleton is composed of discrete plates. Such forms usually carry no record of their early growth. The blastoids studied do show growth lines, but the difficulties involved in trying to reconstruct growth series from them are almost insuperable. For all practical purposes, one must rely on young and old specimens to construct such series. This emphasizes the necessity of complete and

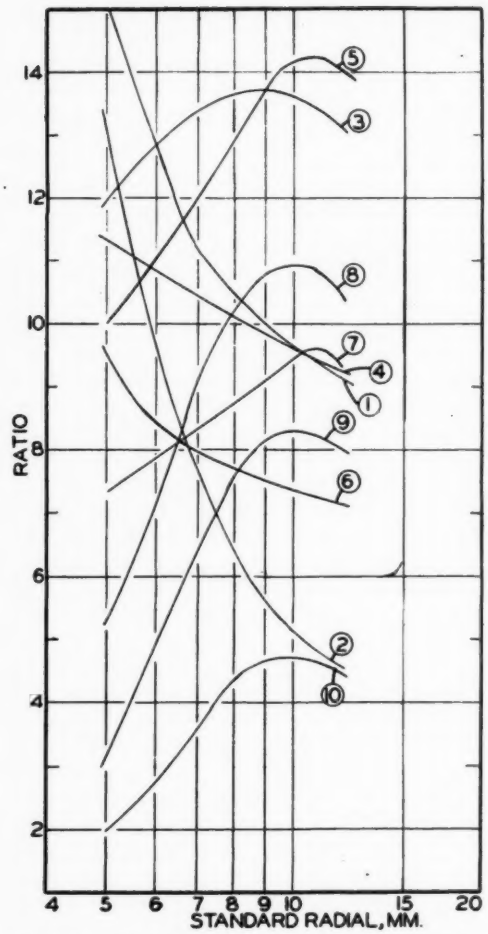


FIG. *14*—Ratios of various characters of *Pentremites pyriformis* as plotted against the standard radial. Each has been multiplied by a constant factor as indicated. 1—number of side plates to length of ambulacrum in mm. (×4); 2—azygous basal to deltoid (×6.7); 3—height to standard radial (×7); 4—side plates to height in mm. (×6); 5—ambulacrum to standard radial (×11); 6—base of radial to standard radial (×12); 7—ambulacrum to height (×14); 8—deltoid to ambulacrum (×2.75); 9—deltoid to standard radial (×16); 10—deltoid to height (×16).

thorough collecting of such forms. (Ulrich made complete collections of some Mississippian blastoids and then described the young forms as separate species.)

Only in post-Meramec rocks are blastoids usually numerous enough for large samples to be collected and, therefore, small samples must be dealt with in many cases. This does not mean that statistical methods cannot be used, but rather that the need for them is increased.

The plate structure of blastoids is quite stable. Therefore, the size and relationships of the plates may be used in studying blastoid species. The "time" character, as usual, is one of primary importance. It was finally decided to use a measurement of the radial plate for this, the independent variable. The radial plate shows a minimum effect of geronticism, and it is as easy to measure as any other plate. A measure of the total height of the calyx would be easier to obtain but it is a composite of many other measures and thus unsatisfactory for this purpose. The particular measure chosen was the length of the outer margin of the left ray of the anterior radial from the lowest part of the base of the deltoid to the top of the basal plate. This measure is termed the *standard radial*. Other measures are as follows: *base of the radial*, from the base of the anterior ambulacrum to the top of the basal below along the surface of the plate; *length of the ambulacrum*, from the lowest part of the notch of the anterior radial to a height equal to the left anterior spiracle; *number of side plates*, counted on the left side and including the spiracle; the length of the *azygous basal*, in its longest vertical dimension; the *height*, from the base of the calyx to the top of the mouth; and the *thickness*, from the surface of anterior ambulacrum horizontally through the specimen at its thickest part to the surface of the posterior interambulacrum.

The ratios between individual characters are often good specific "characters" themselves and ten such ratios for *P. pyriformis* are shown in figure 14. Each curve is nearly a straight-line up to a point where the standard radial length is about 8 mm. At that stage, they tend to change slope markedly and level off, and the ratios become more nearly constant. This is an indication of maturity and *P. pyriformis* may be considered to become mature when the standard radial reaches this length. At the point where the standard radial is about 11 mm. long most of the curves show a rather

definite reversal of trend. This size, therefore, may be considered to mark the beginning of geronticism. The fact that all of these ratios change greatly during growth is very clear.

While measuring the specimens of *P. godoni*, it became evident that the sample of over forty blastoids could be split into two parts, one characterized by a somewhat stellate horizontal section associated with a rather low deltoid to standard radial ratio, and another with a more rounded section and a markedly higher deltoid to standard radial ratio. The first of these will hereafter be referred to as *P. godoni A* and the second as *P. godoni B*. It was believed that the two characters used *could* lead to a valid separation and not a spurious one of the type referred to in the foregoing section on the recognition of synchronous species. The stellate or rounded section has no obvious relationship with the deltoid to standard radial ratio and a correlation between the two might be genetic rather than structural.

When the two sub-samples were plotted on a graph, however, it became evident that they are not at all well separated. Figure 15 is a graph for the base of the radial, which is thoroughly typical of the other characters, plotted against the standard radial. (Data for *P. pyriformis* are included for comparison.) The two sub-samples overlap almost completely but each of the curves for *P. godoni A* is below the comparable ones for *P. godoni B*. Next, these differences were tested for significance. A comparison of the regression lines indicated that the difference is not significant. Because of the constant relationships of the two sets of curves, this test, which compares only a pair of characters may not be conclusive. Therefore, the the more decisive, but more laborious test of significance, that of multivariate analysis, was made. Thus all seven investigated characters of each sub-sample were compared simultaneously to give as nearly as possible a comparison of the fossils as a whole. It revealed that there is less than one chance in one hundred that the two sub-samples, drawn from a population with a variability of the two combined, would differ as much as they actually do. Therefore, *P. godoni A* and *P. godoni B.* probably do differ significantly, and apparently represent two species. The table below lists the equations of the regression lines of these two species:

	P. godoni A	*P. godoni B*
Height	$Y=(1.235, 1.410, 1.615)X^{1.146}$	$Y=(1.202, 1.436, 1.713)X^{1.188}$
Thickness	$Y=(1.233, 1.552, 1.948)X^{1.050}$	$Y=(1.400, 1.640, 1.930)X^{1.068}$
Base of Radial	$Y=(0.356, 0.487, 0.670)X^{1.072}$	$Y=(0.387, 0.507, 0.665)X^{1.087}$
Deltoid	$Y=(0.341, 0.428, 0.540)X^{1.302}$	$Y=(0.353, 0.480, 0.662)X^{1.331}$
Azygous Basal	$Y=(0.185, 0.262, 0.384)X^{1.190}$	$Y=(0.195, 0.270, 0.362)X^{1.222}$
Ambulacrum	$Y=(0.901, 1.052, 1.233)X^{1.318}$	$Y=(0.905, 1.157, 1.475)X^{1.227}$
No. of Side Plates	$Y=(3.45, 4.21, 5.17)X^{1.087}$	$Y=(3.92, 4.97, 6.29)X^{1.068}$

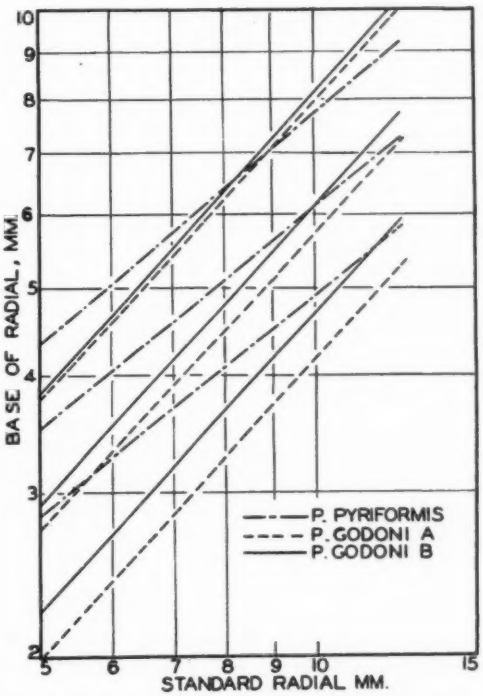


FIG. *15*—Comparison of the ontogenetic development of the base of the radial of *Pentremites pyriformis*, *P. godoni* A and *P. godoni* B. The outer pair of each triad of lines defines the probable limits of variation of that particular population.

Y is the dependent variable, the character listed to the left in the table, and X is the independent variable, the length of the standard radial. In each equation X has three coefficients. The second represents the regression line. The others represent the limiting curves of minimum and maximum variability and are spaced $\pm 3\sigma$ from the regression curve. All equations are based on measurements in millimeters. Thus with

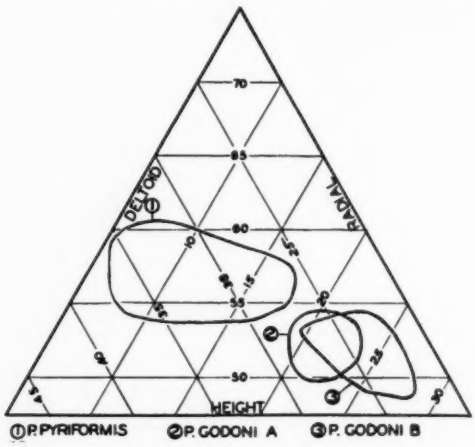


FIG. *16*—Triangular graph showing the relative proportions of the deltoid, radial, and height of *Pentremites pyriformis*, *P. godoni* A, and *P. godoni* B.

these equations, one can measure an unknown specimen and make precise comparison with each of these two species at any growth stage.

The equation for the regression line may be calculated by any standard method such as that given by Simpson and Roe, pp. 262 *et seq.* The maximum and minimum line when plotted on log paper may be calculated more simply. The standard deviation of the sample from its regression line is calculated as discussed in the foregoing section on presentation of data. Points equal to 3σ are measured off above and below a point on the regression line and through these points are drawn two lines parallel to the regression line. Then, using a slide rule with log log scales, the following operations are carried through:

1. Select a point X_1Y_1 on the line in question.
2. On the slide rule, place the sliding index over the value of X_1 on the appropriate log log scale.
3. Move the right or left index of the C scale over this.
4. Move the sliding index over to the exponent of X (this is the exponent of X in the regular regression equation) on the C scale.
5. Read the answer from the appropriate log log scale. These operations have raised X_1 of step 2 to a power, X_1^b.
6. Set the sliding index over the value of Y_1 on the D scale.
7. Move the value of X_1^b (step 5) on the C scale over Y_1.
8. Read the result on the D scale under the right or left index. This is the value of the coefficient a in $Y=aX^b$.
9. The equation for the line in question is, then, $Y=aX^b$, where a is obtained from step 8, and b is the exponent of X in the regression equation.

A further indication of the justification for separating *P. godoni A* and *P. godoni B* is to be found in a triangular graph. Such graphs are a simultaneous plot of three characters but are peculiar in that the measurements of a character must be expressed as a per cent of the sum of all three. Thus it is essentially a graph of proportions. The standard radial, deltoid, and height are plotted against one another in figure 16. The pattern formed by each set of points does not depart widely from circularity. (For the sake of clarity, the individual points are not shown, but only the lines enclosing the areas occupied by the points.) The patterns of *P. pyriformis* and *P. godoni* are completely separated. The pattern of *P. godoni A* and *P. godoni B* overlap considerably, but indicate variation that seems to be distinctly different.

Brachiopods

The brachiopods, like the pelecypods which are considered in the next section, are characterized by having two valves. Each is actually a spiral shell with a very rapid rate of expansion (Thompson, 1942). This is so great that methods used with such spiral shells as the fusulinids are not suitable. The valves often have growth lines so that growth series for many characters, partic-

ularly external ones, can be reconstructed from a few specimens. Changes occurring in the growth of other characters, principally internal ones, cannot be so determined, however. This is probably of small importance in the study of species since internal

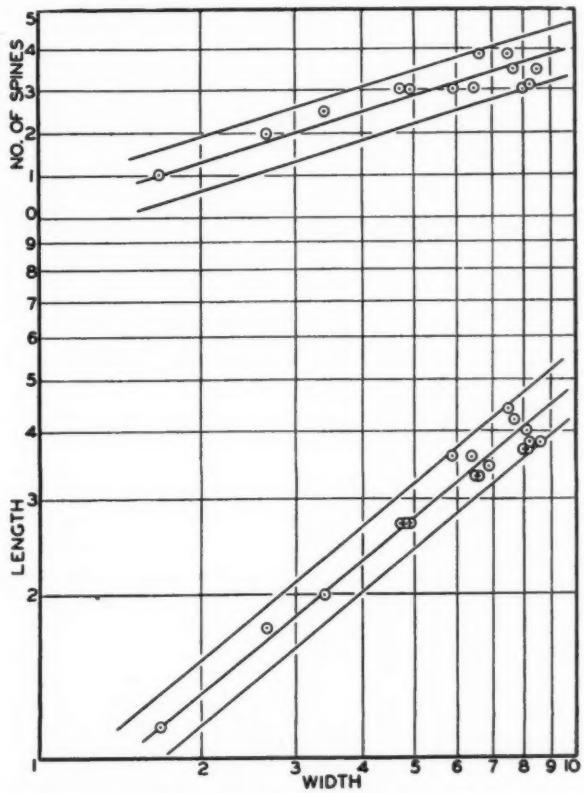


FIG. 17—Graphs of the number of cardinal spines (above) and the length (below) of *Chonetina X*, plotted against the width.

characters generally seem to be rather stable and more suited to the differentiation of genera.

As usual, the choice of a "time" character is a matter of importance. The width at the hinge line is perhaps the first character that might come to mind, but in many brachiopods this is indeterminable. The greatest width is probably about the best character that can be used. In many genera, this occurs at the hinge.

The brachiopod considered here is an undescribed species of *Chonetina* from the Exline limestone in the upper part of the Des Moines series of Livingston County, Missouri. Four characters were studied, the width (at the hinge line), the length, the number of lirae per mm. at the anterior end of the center of the ventral valve, and the number of spines on one side or the other of the beak. Growth lines are absent or discontinuous, so that it was necessary to rely on ordinary growth series. A total of 18 specimens was studied. The ontogenetic development of the length and the number of cardinal spines are shown graphically in figure 17. The number of lirae per mm. is not noticeably related to size, but varies from 5½ to 6 per mm.

This group of specimens, which show no signs of being heterogeneous, may be compared to several species and subspecies of *Chonetina* described by Dunbar and Condra (1932) whose descriptions are qualitative,

though perhaps better than average.

The most noticeable characteristic of the Exline *Chonetina* (hereafter referred to as *Chonetina X*) is its small size at maturity. The largest one measured has a width of less

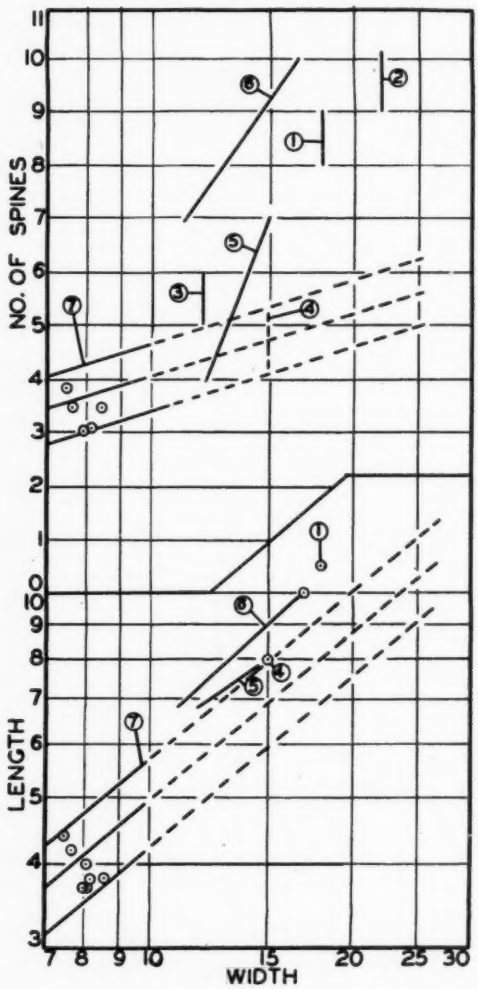


FIG. *18*—Comparison of *Chonetina X* with other Pennsylvanian Chonetinas with respect to number of cardinal spines (above) and length (below). See the text for explanation.

than 9 mm., and it seems doubtful that it attains a width of 10 mm. The length reaches 4.5 mm. and probably does not exceed 5.0 mm. All the other described forms are notably larger, varying from a "mature" width of 12 mm. in *C. flemingi plebia* to 22 mm. in *C. flemingi alata*. The number of cardinal spines of *Chonetina X* does not seem to exceed four on each side of the beak but other forms seem to have 5 to 10 on each side. *C. verneuilianus* may have four but its spines are nearly parallel to the hinge and not steeply oblique as in *Chonetina X*. The number of spines of *C. flemingi crassiradiata* has not been reported. The number of lirae per mm. in *Chonetina X* is 5½ to 6; *C. rostrata* has 6 to 7; *C. flemingi alata* has 4 to 5, and *C. flemingi plebia* has 5½ to 6. Data for other forms are not available.

Chonetina X is most obviously differentiated from other forms by being smaller but size alone must always be used with considerable caution in separating species. The length and number of spines of *Chonetina X* also are decidedly less than in most others. Perhaps, therefore, these specimens are simply dwarfs of some recognized species or "subspecies"?

I do not know of any published consideration that is particularly helpful in pointing out means for identifying dwarfs, which are primarily phenotypic rather than genotypic, with larger specimens of the same species. Therefore, it seems best to assume that if certain specimens are actually dwarfs, normal size might be attained by continuation of growth at its previous rate. This would involve a straight-line extrapolation of the growth curves and such a procedure for *Chonetina X* seems justified. This has been done in the graphs of figure 18 where the length and number of spines are compared with information available for other Chonetinas. In both respects the range of *Chonetina X* seems to fall below those of other Chonetinas but if the curves for *Chonetina X* should turn upward somewhat (if the extrapolation should be curvilinear in the proper degree) some of these ranges might coincide. There is no indication, however, that the curves of *Chonetina X* would actually do so and, on the basis of available data, we are probably justified in concluding that *Chonetina X* of the Exline limestone is not a dwarf but a distinct, undescribed species.

Pelecypods

Pelecypods, like brachiopods, have a test consisting of two rapidly expanding spiral shells. Their measurements are somewhat

standardized. The length is the maximum dimension parallel to the hinge line, the height is the maximum dimension perpendicular to the hinge line, the angle α is measured between the hinge line and the umbonal ridge, and the thickness is measured across the maximum inflation of the two

comya which he examined by statistical methods and concluded to be distinct. Such a graph compares three characters instead of two. Although much used in the physical sciences they have not been employed in biology to any great extent. Construction is as follows: The measures of the three charac-

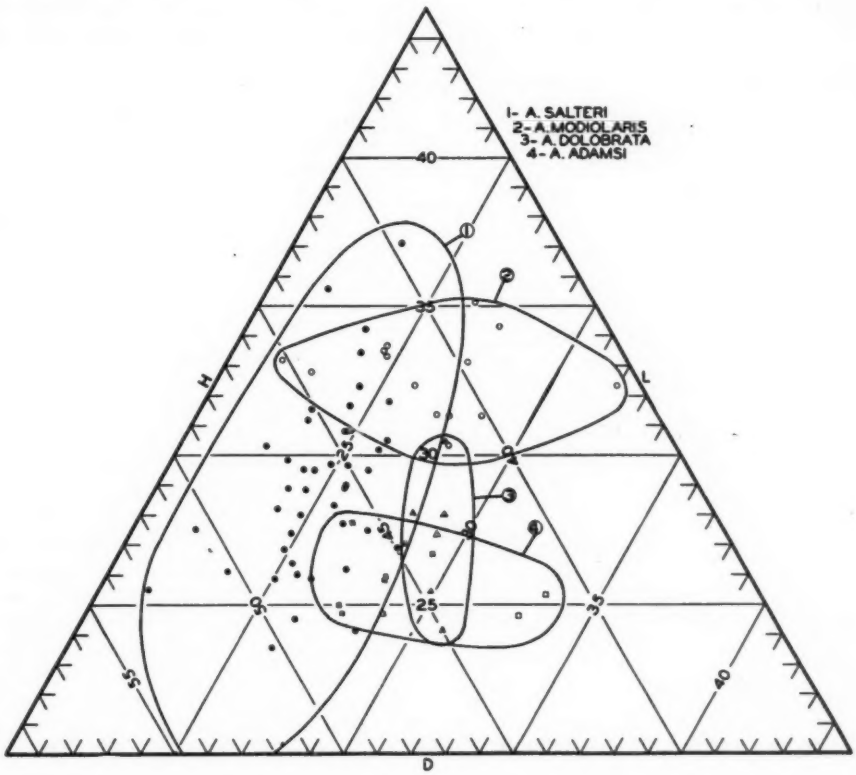


FIG. *19*—Triangular graph of the length, height and distance to maximum down-bulge of four species of *Anthracomya*.

valves. A suitable measure for the "time" dimension in the pelecypods is difficult to obtain. Length, height, and thickness are easily determined but all are commonly subject to gerontic effects. The angle α seems to be less affected, but it cannot be measured accurately and in many forms cannot be measured at all. All things considered, the length probably represents the best compromise for this purpose.

A triangular graph presents the data of Leitch (1940) on four species of *Anthra-*

ters selected are added together for each specimen, and their ratios in per cent are calculated. For example, character $a=2$ mm., $b=3$ mm., and $c=5$ mm.; $a+b+c=10$ mm.; $a=20\%$, $b=30\%$, $c=50\%$ of the whole. These percentages are plotted on the graph which thus shows proportions rather than absolute sizes. In figure 19 the characters used for *Anthracomya salteri.*, *A. modiolaris*, *A. adamsi* and *A. dolobrata* are length, *L;* height, *H;* and distance from the anterior end of the shell to the point of

maximum ventral down-bulge, *D*. A boundary line encloses the field defined by each set of points. Each species clearly occupies a rather definite area, although they overlap to a greater or less extent, and this indicates that we are probably dealing with distinct species.

The distribution fields of the blastoids are more or less circular (fig. 16) but for these pelecypods they are distinctly elongated. This elongation is related to the mode of growth because if the per cent of length is plotted against length (fig. 20), a definite trend in one direction is shown which shifts with growth and this change in proportions with growth is reflected in the triangular graph by an elongation of the fields.

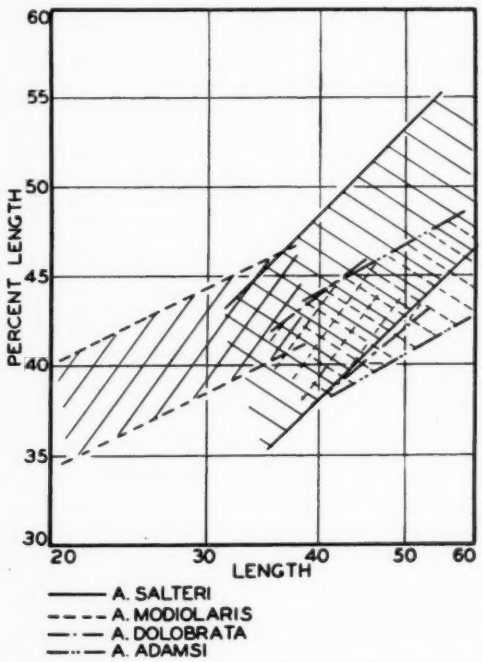


FIG. *20*—Graph of the per cent length used in Fig. 21 plotted against the length for four species of *Anthracomya*.

The fields of *A. salteri* and *A. dolobrata* are elongated in one direction but those of *A. modiolaris* and *A. adamsi* are elongated approximately at right angles. Although the samples of the last three species are not large enough to permit great certainty, the available information indicates that the two groups have different patterns of development. The interpretation to be placed on this is uncertain. Possibly the two groups belong to different phyletic lines but data are not sufficient for a thorough investigation.

The triangular graph seems to have interesting possibilities in the study of fossils. It should not be used to reach definite conclusions, but it may be very helpful in indicating possible relationships and differences.

Gastropods

Spiral shells may be divided into two general groups, the planospiral, represented by the fusulinids and ammonites, and the helicospiral which is characteristic of most gastropods. In the latter group the protoconch is external and unprotected and for this reason it is commonly broken or worn away. In helicospiral shells, therefore, it is generally not possible to make measurements from the beginning point of growth as it is in the fusulinids. It is desirable, however, to use a whorl number as the independent "time" variable, but because the protoconch usually is not available as a beginning, it is necessary to set up another zero point. This may be done as follows: The position where the height of a whorl is exactly three mm., measured parallel to the general shell surface, is found and marked. This is designated whorl number zero. A line passing through this point is then drawn on the shell in the plane which passes through its axis of coiling. This line crosses successive whorls in the direction of the aperture which are designated No. 1, 2, etc. and similarly whorls in the direction of the apex are designated No. -1, -2, etc. This sets up a "time" dimension comparable to that in the other groups of fossils. Selection of a 3 mm. whorl height as the zero point is satisfactory for medium sized shells. A different height may be chosen for groups of larger or smaller species but this should be kept constant within a genus.

The present study is based upon specimens of *Lymnaea stagnalis appressa* Say which were aquarium reared by Dr. Lowell E. Noland of the Zoology department of the University of Wisconsin. Each died a natural death and the size range is typical, therefore, of "mature" individuals. All have the protoconchs preserved and the system of

whorl designation explained above can be checked against the absolute whorl number.

(measured from the external suture to the axis of coiling) and length of body chamber from its maximum downward extension to

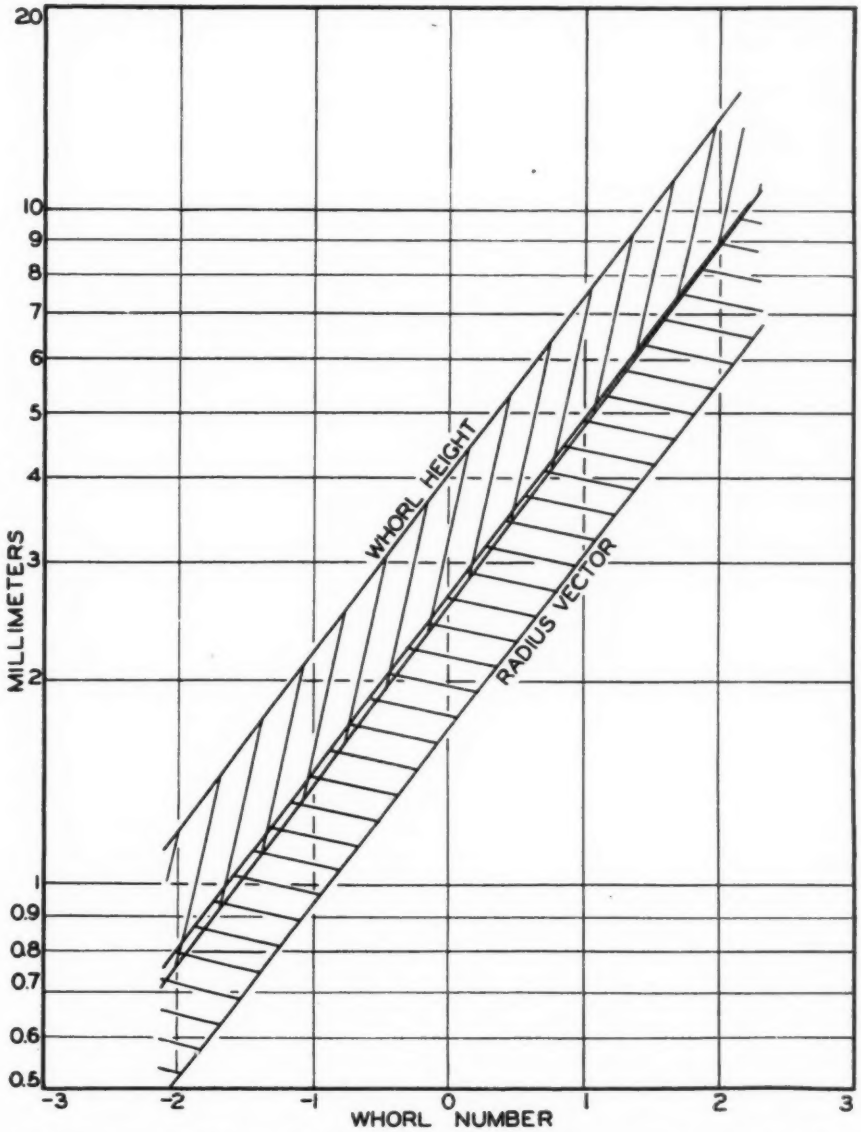


FIG. *21*—Range of variation of the whorl height and radius vector as plotted against the whorl number in *Lymnaea stagnalis appressa*.

These snails are devoid of ornamentation except for growth lines. The following characters, generally measurable in gastropods, were used: whorl height, radius vector

the suture above, parallel to the axis of coiling. The number of actual whorls present in 12 specimens varies from $5\frac{1}{2}$ to $7\frac{1}{2}$ and variation in a natural population would be

at least as great. The designated zero volution occurs at 3 volutions in two specimens, at 3¼ in seven, at 3½ in one, and at 3¾ in two This indicates a satisfactory whorl height to volution number correlation. Figure 21 is a graph of the whorl height and radius vector plotted against the assumed volution number. Figure 22 is a graph of the height of the body whorl plotted against the volution number at the aperture. All show practically

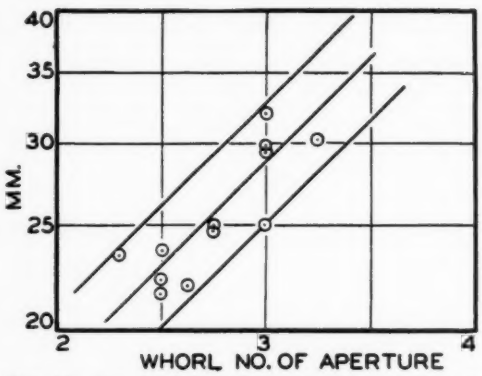


FIG. *22*—Graph of the height of the body whorl of *Lymnaea stagnalis appressa* plotted against the whorl number at the aperture.

straight-line relationships on a semilogarithmic plot. This indicates that the study of gastropods by these methods is entirely practical.

Fusulinids

The fusulinids have, as a group, been treated in a quantitative manner more consistently than any other group of fossils. White, Skinner, Dunbar, Condra, Henbest, Newell, Keroher, Merchant, and Burma, to mention only a few American authors, have all used more or less quantitative methods in dealing with them. These methods have been used in a rather timid manner, however, and a qualitative attitude toward the data has always been evident. For example, the writer (Burma, 1942) published a paper on the *Triticites* in which a quantitative handling of the data was attempted. This attempt was half-hearted, however, and deservedly failed. An effort was made to define species on the basis of their variation, which was certainly worth while, but the variation was handled in an essentially qualitative manner. Also, no effort was made to compare species except in a qualitative manner and, consequently, it seems certain that some of the species erected were distinguished on inadequate grounds and are probably invalid.

The methods of measuring fusulinids seem adequate for most purposes. The following data are commonly reported: half length (or total length), radius vector (or total width), form ratio, tunnel angle, wall thickness, height of volution, septal count per volution, and diameter of proloculum. Each measure is reported in relation to volution number, which is another character reflecting the rate of expansion of the spirotheca. The spiral is essentially logarithmic and therefore the length of the spirotheca in successive volutions is described by an exponential function and the volution number should be plotted on an arithmetic scale in making graphs. This character is universally used as a "time" character in fusulinids and seems to be well fitted to the purpose.

The half length is measured on axial sections along the axis of coiling from the center of the proloculum to the extremity of a volution. Some authors have used the total length and there is no *a priori* reason for selecting one rather than the other except that the half length is preferable if the form ratio is to be considered.

The radius vector can be measured on either axial or saggital sections. In actual practice, it should be measured on both, the first being used to compute the form ratio, and the second for reporting the character itself as explained below. In either case the radius vector is the measure of the logarithmic spiral of the spirotheca from the center of the proloculum to the exterior of a volution perpendicular to the axis of coiling. Some authors have reported the full width which is the sum of a radius vector of one volution and that of another 180° from it. The radius vector is more significant biologically and mathematically than the total width and there are other reasons for preferring it.

The form ratio is the ratio of the half length to the radius vector (or total length to total width). It is usually reported as a single figure, e.g., 2.0 meaning that the half

length is twice the radius vector. A total length to width ratio has been used by some authors but this is a compound measure which is less significant biologically. The length is a valid character, and may be measured at any growth stage but the width is the sum of the radius vectors of two growth stages half a volution apart. If is a compound measure, being a function of the width of the tunnel and the radius vector. As such it is undesirable, but it is so firmly entrenched that it seems hopeless to attempt to substitute the width of the tunnel, a more meaningful measure, for it.

The wall thickness can be measured on either axial or saggital sections. For the sake

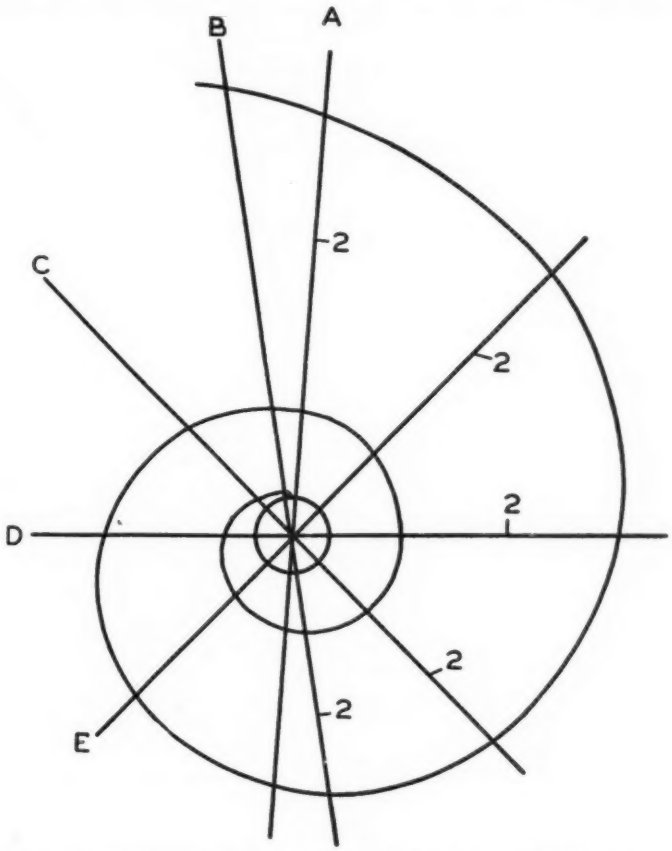


FIG. *23*—Diagrammatic saggital cross-section of a fusulinid showing various planes in which an axial section might be cut.

species are to be compared by multivariate analysis, the form ratio should not be used, as this would introduce duplication of data, increase the complexity of calculation and gain nothing.

The tunnel angle is the angle subtended by lines joining the sides of the tunnel with the center of the proloculum. It can be measured only on the axial sections. This of accuracy (see below), it should always be measured on saggital sections.

The height of volution is the distance from the outside of one volution to the outside of the next. It gives no information not implicit in the radius vector. Although almost universally reported, its usefulness is very limited. Like the septal count it should be measured on saggital sections.

The diameter of the proloculum is a very useful specific character but because few sections are perfectly centered it is difficult to use in a multivariate analysis.

As indicated above, the accuracy and reliability of measurements obtained from axial and saggital sections differ greatly. Saggital sections show the entire coil of the spirotheca and measurements made on them can be referred to a definite volution and thus to a definite growth stage. The axial sections, however, are unoriented. They may coincide with an infinity of planes each of which cuts the spirotheca in a different place. Thus in figure 23, any line segment labeled "2" might be reported as the height of the second volution. Thus measurements made on axial sections can not be accurately located and they may be expected to show greater, though spurious, variation than do those on the saggital sections. In a sample their planes may or may not be evenly distributed through 180 degrees. In one sample such sections might cluster around the orientation shown by plane *C* in figure 23, and in another around plane *A*. The tunnel angles of these two samples would not be comparable because they would show development at stages 135 degrees apart and they might erroneously indicate a nonexistent difference.

As an example comparison is made between actual measurements of *Triticites secalicus* and *T. primarius*. Measurements of the former were made from topotype specimens, and of the latter from specimens on the slides used in the original description of the species by Merchant and Keroher (1939). The following comparisons are for the fifth volution:

	T. primarius	*T. secalicus*	*Comparison*
Axial sections			
Radius Vector	$M=$ 0.788 mm.	$M=$ 0.613 mm.	$d/\sigma_d=3.77$ (0.67)
	$\sigma=$ 0.121 mm.	$\sigma=$ 0.990 mm.	$P=0.999$ (0.497)
Half length	$M=$ 2.338 mm.	$M=$ 1.589 mm.	$d/\sigma_d=4.49$ (1.39)
	$\sigma=$ 0.415 mm.	$\sigma=$ 0.413 mm.	$P=0.9999$ (0.835)
Tunnel Angle	$M=46.0°$	$M=53.1°$	$d/\sigma_d=6.02$ (2.92)
	$\sigma=$ 5.0°	$\sigma=10.35°$	$P=0.99999$ (0.997)
Saggital sections			
Radius Vector	$M=$ 0.724 mm.	$M=$ 0.698 mm.	$d/\sigma_d=0.67$
	$\sigma=$ 0.071 mm.	$\sigma=$ 0.108 mm.	$P=0.497$
Wall thickness	$M=$ 0.062 mm.	$M=$ 0.073 mm.	$d/\sigma_d=4.47$
	$\sigma=$ 0.007 mm.	$\sigma=$ 0.125 mm.	$P=0.9999$
Septal count	$M=21.3$	$M=20.2$	$d/\sigma_d=1.23$
	$\sigma=$ 1.96	$\sigma=$ 2.36	$P=0.781$

As usual, a value of $d/\sigma_d=3.0$ or more is considered to be significant. (t is a better measure here but leads to the same results.) In the axial sections the radius vector indicates the probability (P) that the two samples are different is 0.999 but the probability indicated by the saggital sections is only 0.497. Thus the axial sections greatly exaggerated the difference between these species probably as a result of inaccurate orientation.

Since the radius vector for the axial sections should show the same significance as the radius vector for the saggital sections, we may subtract 3.10 from the axial significance to reduce it to 0.67 as in the saggital sections. If we subtract the same amount from the significance figures for the half length and tunnel angle, their significance, shown in parentheses, is 1.39 and 2.92 respectively. (This method of treatment is very approximate, but it is probably as accurate as the data warrant.) These figures suggest that the radius vectors, half lengths, and septal counts of *T. primarius* and *T. secalicus* do not differ significantly but that the tunnel angles and wall thicknesses do. It is very common for different stratigraphic occurrence of fusulinids to be made the basis of different specific names. These two species, barely separable morphologically, are separated by eight cyclothems and the Missouri Virgil unconformity.

Such similarity of widely separated *Triticites* suggests the advisability of checking some species which occur closer together. For this purpose, *T. collus* of the Cement City limestone and *T. caccus* of the Argentine limestone, separated by only one or two cyclothems and both described by me

in 1942, were compared by multivariate analysis and the difference between them was found to be completely insignificant. These results are as important as they are unexpected. Although *T. collus* and *T. caccus* have similar measures, they differ from one another as much as a great many other fusulinid species. Consequently the entire classification of fusulinids on the species level appears to be questionable and almost certainly the fusulinids have been over-finely split.

CONCLUSION

The foregoing outline of quantitative invertebrate paleontology does not cover this field thoroughly and much remains to be done. However, some conclusions stand out clearly. Paleontological collections are samples. For valid results they *must* be recognized as such and treatment on any other basis is inadequate and likely to produce erroneous conclusions. Paleontology should be concerned with genetic units and eternal vigilance is required to prevent the recognition of morphological sections of intergrading populations as valid units. Fossils should be studied as growing, developing organisms, for otherwise comparisons will be made on very dubious grounds. Species are variable and this variability is an important characteristic of species. Certainly it is time for paleontologists to cease merely labeling specimens and to become paleobiologists.

BIBLIOGRAPHY

BANCROFT, B. B., 1945, The brachiopod zonal indices of the stages Costonian to Onnian in Britain: Jour. Paleontology, vol. 19, pp. 181–252.

BURMA, B. H., 1942, Missourian *Triticites* of the northern Mid-continent: Jour. Paleontology, vol. 16, pp. 739–755.

CARRUTHERS, R. G., 1910, On the evolution of *Zaphrentis delanouai* in Lower Carboniferous time: Quart. Jour. Geol. Soc. London, vol. 66, pp. 523–538.

COOPER, C. L., 1945, Moult stages of the Pennsylvanian ostracod *Ectodemites plummeri*: Jour. Paleontology, vol. 19, pp. 368–375.

DAVIES, J. H., and TRUEMAN, A. E., 1937, A revision of the non-marine lamellibranchs of the Coal Measures: Quart. Jour. Geol. Soc. London, vol. 83.

DOBZHANSKY, T., 1941, Genetics and the origin of species: Columbia University Press, 2nd edit., 446 pp.

DUNBAR, C. O., and CONDRA, G. E., 1932, Brachiopods of the Pennsylvanian system in Nebraska: Nebraska Geol. Survey, 2nd ser., Bull. 5, 377 pp.

ELIAS, M. K., 1937, Stratigraphic significance of some late Paleozoic fenestrate bryozoans: Jour. Paleontology, vol. 11, pp. 306–334.

JEFFORDS, R. M., 1947, Pennsylvanian lophophyllidid corals: Univ. Kansas, Pal. Contrib. no. 1, 84 pp.

LEITCH, D., 1936, The *Carbonicola* fauna of the Midlothian 5-foot coal, a study in variation: Trans. Geol. Soc. Glasgow, vol. 19.

——, 1940, A statistical investigation of the Anthracomyas of the basal similis-pulchra zone in Scotland: Quart. Jour. Geol. Soc. London, vol. 96, pp. 13–36.

MAYR, E., 1942, Systematics and the origin of species: Columbia University Press, 334 pp.

NICOL, D., 1944, New West American species of the foraminiferal genus *Elphidium:* Jour. Paleontology, vol. 18, pp. 172–185.

ROWLANDS, T. H., 1928, Studies in the variation of *Batillaria pleurotomoides:* Geol. Mag., vol. 65, pp. 530–541.

SALMON, E. S., 1942, Mohawkian Refinesquinae: Jour. Paleontology, vol. 16, pp. 564–603.

SCHENCK, H. G., 1945, Geologic application of biometrical analysis of molluscan assemblages: Jour. Paleontology, vol. 19, pp. 504–521.

SCOTT, GAYLE, 1924, Some gerontic ammonites of the Duck Creek formation: Texas Christian Univ. Quart., vol. 1, pp. 1–31.

SIMPSON, G. G., 1941, Range as a zoological character: Am. Jour. Sci., vol. 239, pp. 785–804.

——, 1944, Tempo and mode in evolution: Columbia University Press, 237 pp.

——, and ROE, A., 1939, Quantitative zoology: McGraw-Hill, 414 pp.

STUART, A., 1927, Ontogenetic and other variation in *Volutonina spinosa:* Geol. Mag., vol. 64 pp. 545–557.

THOMPSON, D'A. W., 1942, On growth and form: Cambridge University Press, 2nd ed., 1116 pp.

TRUEMAN, A. H., 1922, The use of *Gryphaea* in the correlation of the Lower Lias: Geol. Mag., vol. 59, pp. 256–268.

——, 1924, The species concept in paleontology: Geol. Mag., vol. 61, pp. 355–360.

WADDINGTON, C. H., 1929, Notes on graphical methods of recording dimensions of ammonites: Geol. Mag., vol. 66, pp. 180–186.

WILLARD, B., 1930, Some evolutionary stages of *Platystrophia:* Jour. Paleontology, vol. 4, pp. 29–32.

WILLIAMS, R. W., 1940, On "type" specimens: Ann. Ent. Soc. America, vol. 33, pp. 631–624.

WOOD and BARNARD, 1946, *Ophthalmidium:* a study of nomenclature, variation, and evolution in the Foraminifera: Quart. Jour. Geol. Soc. London, vol. 52, pp. 77–107.

JOURNAL OF PALEONTOLOGY, VOL. 22, NO. 6, PP. 762–766, PLS. 116–117, NOVEMBER 1948

EOCENE ALGAE FROM FLORIDA

J. HARLAN JOHNSON AND BERNARD J. FERRIS
Colorado School of Mines, Golden, Colorado

ABSTRACT—Coralline algae were obtained from samples from a well drilled in Duval County, Florida. They came from the *Dictyoconus americanus* zone of the upper middle Eocene. The following species are described: *Archaeolithothamnium parisiense* Lemoine, *A. dalloni* Lemoine, *A. floridanum* n. sp., *A. gunteri* n. sp., *Lithophyllum compactum* n. sp., *L. zonatum* n. sp., *Amphiroa americana* n. sp. In addition, fragments of several other species of *Archaeolithothamnium*, *Lithophyllum* and *Lithothamnium* were observed. This flora is of interest because these species are the first Eocene coralline algae to be described from the Atlantic or Gulf Coasts of the United States.

INTRODUCTION

THE Eocene calcareous algae of North America have received very little study. Only three papers (Howe 1918, 1919, and 1934) have so far been published describing them and only one is concerned with a flora from the United States (Sierra Blanca limestones of California).

Several geologists writing on the stratigraphy of California have mentioned the occurrence of algae in Eocene rocks without describing them. Also, for a number of years some Gulf Coast geologists and micropaleontologists have recognized the presence of coralline algae in well cuttings, but this material has never been studied.

During 1945 the Florida Geological Survey sponsored a careful study of samples from Florida wells. In the course of this study algae of several types were found and sent to Dr. Johnson. The material described in this paper was all obtained from two well samples from well No. 544, drilled in Duval County a few miles north of Jacksonville. Samples from 970 and 990 feet contain an abundance of algal material which probably makes up about 30 per cent of the latter sample. These specimens occur in tan granular limestone of the *Dictyoconus americanus* zone of the upper Middle Eocene.

Acknowledgements

The authors are grateful to Herman Gunter and the Florida Geological Survey for furnishing the material and some of the thin sections. The Colorado School of Mines supplied laboratory and photographic facilities.

THE ALGAE

Classification

Madame Lemoine, who is undoubtedly the foremost living student of coralline algae, fossil and modern, has worked out a classification in which specific differences are based on the dimensions of the cells which form the tissues, and the size, shape and arrangement of the spores and spore cases. This classification has been adopted by all students of fossil algae. The general outline of this classification is shown in the accompanying table.

The Florida material contains representatives of the genera *Archaeolithothamnium*, *Lithophyllum*, *Lithothamnium*, and *Amphiroa*.

SYSTEMATIC DESCRIPTIONS

Family CORALLINACEAE
Sub-family MELOBESIEAE
Genus ARCHAEOLITHOTHAMNIUM Rothpletz

Fragments of algae belonging to this genus are the most abundant forms occurring in our collection.

This genus is characterized by a tissue the cells of which usually are arranged in well-defined rows and the sporangia are usually numerous and regularly spaced in a row or in several parallel rows. Usually the cell arrangement is very regular. However, sometimes irregular arrangement occurs with the result that it may be impossible to decide whether fragments belong in this genus or in *Lithothamium*, unless the fruiting can be observed. Several of our specimens clearly show the fruiting.

Numerous fragments possess tissue which indicates that they belong to this genus. Only those showing sporangia or those of unusual size or arrangement of cells are described. At least two other species also occur.

long by 0.044 to 0.045 mm. wide. These features all fit within the description and the dimensions of *Archaeolithothamnium parisiense* (Gümbel) as redefined and described by Lemoine (1923) from the Eocene of the Paris Basin of France.

TABLE 1.—General classification of the coralline algae after Madame Lemoine

	Sub-families:	Genera:
Class RHODOPHYTA Family CORALLINACEAE:	(A). Melobesieae:	1. *Archaeolithothamnium.* 2. *Mesophyllum.* 3. *Lithophyllum.* 4. *Epilithon.* 5. *Melobesia.* 6. *Tenarea.* 7. *Lithothamnium.* 8. *Porolithon.* 9. *Pseudolithophyllum.*
	(B). Corallineae:	1. *Amphiroa.* 2. *Arthrocardia.* 3. *Corallina.* 4. *Cheilosporum.* 5. *Jania.*

ARCHAEOLITHOTHAMNIUM PARISIENSE
(Gümbel)
Plate 116, figures 1 and 2

Lithothamnium parisiense GÜMBEL, C. W., Die sog. Nulliporen. Abh. des K. bayer. Akad. d. Wiss. II, band XI, Abh. 1, München 1871, p. 32, pl. 11, fig. 8-ab.

Lithothamnium parisiense ROTHPLETZ, A., Fossile Kalkalgen. Deuts. Geol. Gesell. Zeitschr., vol. 43, part 2, p. 304, 1891.

Archaeolithothamnium parisiense LEMOINE, Melobesiées du Calcaire Pisolitic. Soc. Geol. France Bull. 4 ser., vol. 23, pp. 63–65, figs. 1–3, 1923.

Description.—Fragments of an irregularly mammillated or branching thallus. Tissue composed of rather irregular rows of cells.

Rows of cells were measured cell by cell at intervals from the base to the tip of a specimen. The following figures show the range of cell dimensions:

18–23μ long, 12–15μ wide (row near base)
19–25 long, 12–15 wide (row near base)
25–29 long, 8–12 wide (row near base)
28–31 long, 16–17 wide (row near base)
32–36 long, 25–30 wide (row near base)
27–31 long, 30–37 wide (row near top)
22–25 long, 12–20 wide (average)

Sporangia ovid, rather gibbous; in staggered rows of 8 to 15 (fig. 2). They measure 0.046 to 0.098 mm. long and 0.039 to 0.057 wide; the average size is 0.039 to 0.057 mm.

Illustrated specimen from Slide #1232 Johnson Collection of fossil algae, Colorado School of Mines.

ARCHAEOLITHOTHAMNIUM FLORIDANUM
Johnson and Ferris, n. sp.
Plate 117, figure 4

Description.—This species is represented by several fragments which appear to belong to a form with thick stubby branches or mammillae. The tissue consists of cells in regular rows with continuous vertical partitions producing a very regular pattern. The cells are quite uniform in size averaging about 0.033 by 0.014 mm. but showing a range from 0.026 to 0.036 mm. long and 0.012 to 0.019 mm. wide. The sporangia are evenly spaced in regular rows. One specimen shows several rows (pl. 117, fig. 4). They are elliptical and measure 0.084–0.109 mm. long and from 0.052 to 0.067 wide (average 0.094 by 0.063).

Remarks.—The nearest described species is *A. dalloni* Lemoine from Algeria. Its cells are different in size and proportionally wider. Its sporangia are differently shaped and slightly different in dimensions. It also appears to develop long, slender branches.

Type specimen.—Slide 2–5, Johnson Collection, Colorado School of Mines.

ARCHAEOLITHOTHAMNIUM DALLONII
Lemoine
Plate 116, figure 5

1939—Mémoire Paleont., No. 9, Service Carte Geol. Algerie, pp. 57–58, pl. 1, fig. 2, text fig. 23, 24, p. 62.

Description.—Fragments of a branching form. Tissue composed of regular rows of large elongated cells. The longitudinal walls are much more distinct than the transverse walls. As a result the tissue shows well defined longitudinal rows of cells but only vague suggestions of horizontal rows. Cell dimensions: 0.0331 to 0.0423 mm. long averaging 0.04 mm., and 0.0126 to 0.0153 mm. wide averaging 0.0144. Sporangia are rare; only a few occur in a row. They are elliptical to gourd-shaped and measure 0.071 to 0.102 mm. long and 0.057 to 0.079 mm. wide.

Remarks.—A few Florida specimens fit Lemoine's description of *A. dallonii* so exactly that there can be no hesitation in referring them to this species.

Type specimen.—Slide 1265, Johnson Collection, Colorado School of Mines.

ARCHAEOLITHOTHAMNIUM GUNTERI
Johnson and Ferris, n. sp.
Plate 116, figure 3

Description.—The fragments indicate a mammillated form which developed either thick crusts or nodular masses. Tissue consists of rows of cells with well defined longitudinal and transverse walls; the horizontal walls being more strongly developed.

Cell dimensions.—Length 0.013 to 0.020 mm., averaging 0.018, and width 0.007 to 0.013 mm., averaging 0.01 mm. Sporangia long and narrow, rectilinear ovid, arranged in long, closely packed rows. Dimensions of sporangia: length 0.061 to 0.079 mm., averaging 0.066 mm., and width 0.024 to 0.041 mm., averaging 0.033 mm.

Note.—This species suggests *A. lugeoni* Pfender but differs in having much narrower sporangia, slightly narrower cells, and by developing much thicker tissues. It has been named in honor of Herman Gunter, Director of the Florida Geological Survey.

Type specimen.—Slide 1123a, Johnson Collection, Colorado School of Mines.

ARCHAEOLITHOTHAMNIUM sp.
Plate 116, figure 4

Description.—This specimen is a well preserved fragment of tissue composed of cells arranged in orderly rows that are slightly arched in the section. The vertical partitions are more conspicuous than the horizontal. The cells are rectangular, measuring 0.021 to 0.027 mm. long by 0.009 to 0.0144 mm. wide, averaging 0.025 by 0.012 mm. No conceptacles are present on this specimen.

Remarks.—The cell dimensions suggest *A. nummuliticum* (Gümbel) Rothpletz but since the specimen contains no conceptacles and gives little indication of the shape of the branches no attempt is made to identify it.

Type specimen.—Slide 2–4, Johnson Collection, Colorado School of Mines.

Genus LITHOPHYLLUM Philippi

Numerous fragments of tissue showing structure indicative of this genus were found. In order of abundance they rank next to fragments of *Archaeolithothamnium*. Differences in texture and cell dimensions suggest that several different species are represented. Most of the fragments do not show conceptacles and their dimensions and patterns are common to several described species which are differentiated on the basis of conceptacles. Only those which show conceptacles or have unusual and distinctive cell measurements or structures are discussed.

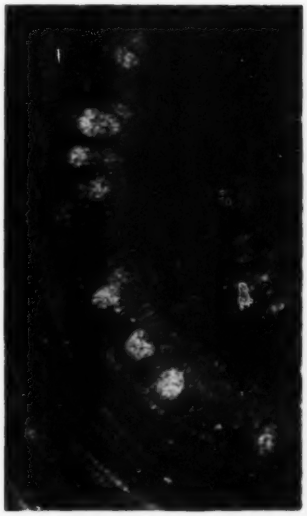
LITHOPHYLLUM COMPACTUM Johnson and Ferris, n. sp.
Plate 117, figure 1

Description.—Tissue a compact mass of rectangular cells. The cells of the central

EXPLANATION OF PLATE 116

FIG. *1—Archaeolithothamnium parisiense* Lemoine ×25. General view of tissue and spores. (p. 763)
2—Archaeolithothamnium parisiense Lemoine ×75. Detail of cells and spores. (p. 763)
3—Archaeolithothamnium gunteri Johnson and Ferris n. sp. ×75. Detail of tissue and spores. (p. 764)
4—Archaeolithothamnium sp. (long. section) ×75. (p. 764)
5—Archaeolithothamnium dallonii Lemoine ×75. Detail of cells and spores. (p. 764)

1



2

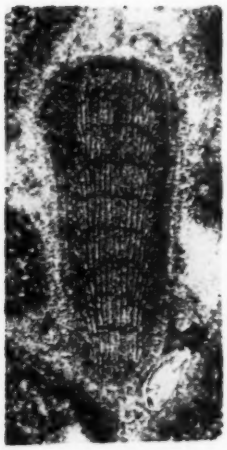
3

4

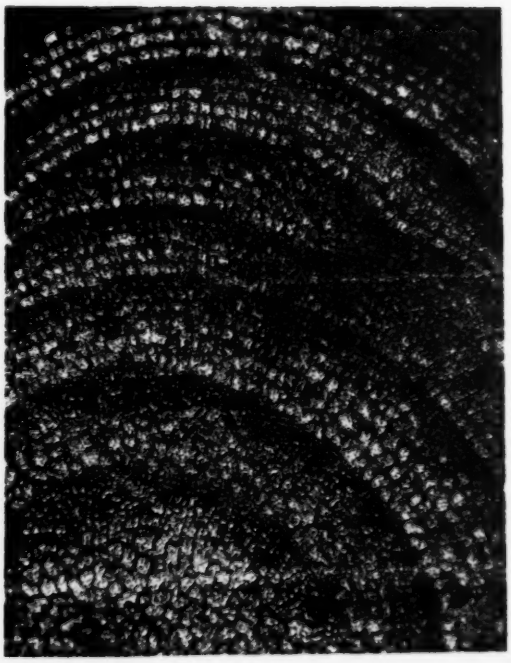
5

Johnson and Ferris, Eocene coralline algae

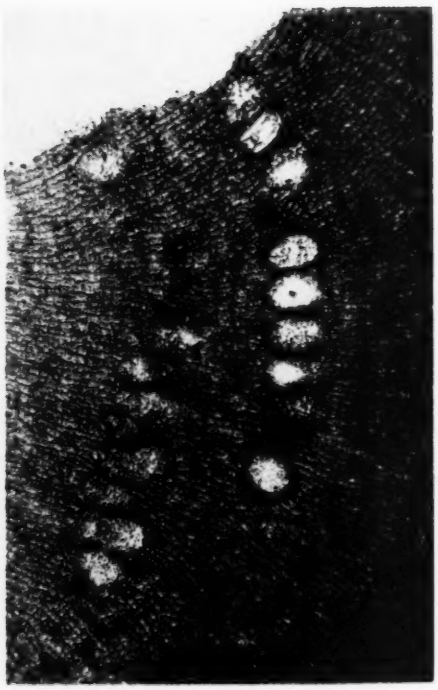
1



2



3



4

Johnson and Ferris, Eocene coralline algae

portion, the central or medullary hypothallus, are arranged in concentric arched rows a number of which form a growth layer. However, the growth layers are not as conspicuous as in many other species of this genus. Bordering the arched layers of the hypothallus are nearly vertical layers of the perithallus.

The cells of the hypothallus are quite constant in size, measuring 0.0081 mm. to 0.0108 mm. (average 0.009 mm.) wide and 0.0216 mm. to 0.027 mm. (average 0.025 mm.) long. The perithallus is composed of cells measuring 0.025 to 0.033 mm. long (average 0.0306 mm.), and 0.009 to 0.0117 mm. wide (average 0.0099 mm.).

A conceptacle is 0.363 mm. long by 0.171 mm. wide.

Remarks.—*L. compactum* in general appearance closely resembles *L. homogenum* Howe but differs in having much larger cells forming the perithallus.

Type specimen.—Slide 1266, Johnson Collection, Colorado School of Mines.

LITHOPHYLLUM ZONATUM Johnson and Ferris, n. sp.
Plate 117, figure 3

Description.—Tissue shows well-defined, strongly-arched layers or zones, each composed of a number (usually five) rows of cells. Each layer represents a period of growth. Outermost row of each layer shows stunted cells. The other layers show well-developed cells regularly arranged in rows. Cell dimensions in the regular rows: length 0.023 to 0.032, averaging 0.027 mm., width 0.013 to 0.034 mm., averaging 0.025. In stunted rows the average width diminishes to 0.012 and lengths to 0.015 mm. Conceptacles unknown.

Remarks.—The distinctive features of this species are the nearly square cells, the strongly developed growth zones and the cell dimensions. The cell dimensions differ appreciably from those of any previously described form known to the writers.

L. simplex Lemoine has cells which are only slightly smaller in size, but shows an entirely different tissue structure.

Type specimen.—Slide 1027, Johnson Collection, Colorado School of Mines.

Genus LITHOTHAMNIUM Philippi

Several shreds of tissue belonging to this genus have been observed. All appear to represent thin encrusting forms. None of the specimens shows conceptacles and all are so small and fragmentary that it seems desirable only to record their presence.

Sub-family CORALLINEAE
Genus AMPHIROA (Lamouroux)

The collection contains several segments which clearly belong to this genus. Most of them are small and badly frayed and do not warrant description. One specimen, however, shows a complete segment with cell dimensions differing from any species hitherto known.

AMPHIROA AMERICANA Johnson and Ferris, n. sp.
Plate 117, figure 2

Description.—Segments composed of 9 to 16 parallel rows of long narrow cells. Rows horizontal in central portion with sharp angular curves near margins.

Cell measurements in alternate rows are as follows:

Top—	height 57–71μ	width 10–13μ
	height 56–72	width 11–13
	height 56–70	width 10–13
	height 68–71	width 11–13
Base—	height 64–68	width 10–11

Dimension of segments 0.557 mm. long and 0.143 to 0.23 wide. No conceptacles were observed but in this genus they are terminal and not likely to be preserved in fossils.

Remarks.—There have been considerable differences of opinion among phycologists as to the distinction between this genus and *Arthrocardia*. Among modern forms the posi-

---

EXPLANATION OF PLATE 117

FIG. *1*—*Lithophyllum compactum* Johnson and Ferris n. sp. (long. section) ×75. Showing character of tissue and conceptacle. (p. 764)
2—*Amphiroa americana* Johnson and Ferris n. sp. (long. section) ×75. (p. 765)
3—*Lithophyllum zonatum* Johnson and Ferris n. sp. (slightly oblique section) ×75. (p. 765)
4—*Archaeolithothamnium floridanum* Johnson and Ferris n. sp. (long. section) ×75. (p. 763)

tion and arrangement of the conceptacles are of primary importance in classification. Since the conceptacles are missing in the fossil form the diagnosis must be based on the size and arrangement of cells. With only one fragment of this species available for study it seems best to place it in the broader group of *Amphiroa*, although the shape of the cell rows suggests *Arthrocardia* as described by Lignac-Grutterick (1943).

Type specimen—Slide 2–1, Johnson Collection, Colorado School of Mines.

REFERENCES

HOWE, M. A., 1918, Contributions to the geology and paleontology of the Canal Zone, Panama, and geologically related areas in Central America and the West Indies: on some fossil and Recent Lithothamneae of the Panama Canal Zone: U. S. Nat. Museum Bull. 103, pp. 1–12.

——, 1919, Tertiary calcareous algae from the Islands of St. Bartholomew, Antigua, and Anguilla: Carnegie Inst. Wash. Pub. 291, pp. 9–19, 6 pls.

——, 1934, Eocene marine algae from the Sierra Blanca limestone: Geol. Soc. America Bull., vol. 45, pp. 507–518, 5 pls.

LEMOINE, MME. P., 1923, Contribution a l'etude des corallinacées fossiles, VI, les Melobesiees du calcaire pisolitic du Basin de Paris: Soc. Géologique de France, 4th ser., vol. 23, pp. 62–69.

——, 1939, Les algues calcaires fossiles de L'Algerie, materiaux pour la Carte geologique de L'Algerie: 1st ser. Paleontologie, No. 9, 130 pp., 3 pl.

LIGNAC-GRUTTERINK, L. H., 1943, Some Tertiary Corallinaceae of the Malaysian Archipelago: Verk. Geol. Mynb. gen. Geol. Serie, deel 13, pp. 283–297, 2 pls.

MANZA, A. V., 1940, A revision of the genera of articulated corallines: Philippine Jour. Science, vol. 71, pp. 239–313.

JOURNAL OF PALEONTOLOGY, VOL. 22, NO. 6, PP. 767–773, PL. 118, NOVEMBER 1948

SOME PENNSYLVANIAN CONODONTS FROM IOWA

WALTER YOUNGQUIST AND BRUCE C. HEEZEN
University of Idaho and Columbia University

ABSTRACT—A small but well preserved conodont assemblage has been collected from a thin Pennsylvanian shale in south-central Iowa. These conodonts represent eight genera and thirteen species. Only a few studies of Late Paleozoic conodonts have been published, and therefore the exact stratigraphic position of this fauna is uncertain. Nevertheless, the few specimens that compare closely or are conspecific with previously described forms indicate that the containing beds are most probably equivalent to the Cherokee shale (lower Des Moines) of Missouri. The absence of the genus *Gondolella*, however, suggests that the assemblage may possibly be pre-Des Moines in age.

No studies of Pennsylvanian conodonts from Iowa have so far been published and as C. L. Cooper (1947, p. 269) has pointed out, paleontological literature includes relatively few papers on Pennsylvanian conodonts from anywhere. An indication of the occurrence of conodonts in the Pennsylvanian of Iowa was made, however, as early as 1928 by V. H. Jones (unpublished master's thesis, State Univ. of Iowa) in a faunal list in which he noted their presence in the Deer Creek limestone member of the Shawnee formation (Missouri series) in southwestern Iowa. In 1946, Mr. C. B. Campbell of Knoxville, Iowa, called the writers' attention to the presence of conodonts in Pennsylvanian shales near that city. Specimens which were collected by the writers in company with Mr. Campbell during the fall of 1946 constitute the basis for the present report.

Although a large number of shales were sampled, conodonts were found at only two places. The better locality is about three-quarters of a mile northwest of Knoxville, in the NW¼ sec. 1, T. 75 N., R. 20 W., Marion County, Iowa. At this place conodonts can be seen with the aid of a hand lens in thin-bedded, black, somewhat slaty shale in association with abundant fish remains, including shark spines. For effective study, the platform type of conodonts (which make up the bulk of this fauna) must be free from matrix. This black shale does not yield conodonts readily and therefore some of the less indurated marine shales stratigraphically close to the black shale were also sampled. A single bed of gray-green shale about 8 inches thick and some 2 feet stratigraphically higher than the black conodont-bearing shale also was found to contain conodonts in moderate abundance.

The name of the stratigraphic unit which yielded the conodonts could not be ascertained with certainty. The region is largely drift-covered and commonly the beds in a given exposure cannot be traced for more than a few yards. These conodont-bearing beds crop out in the middle portion of a small ravine which is tributary to White Breast Creek. The strata in the lower portion of the ravine are essentially flat-lying. Those in the upper part, however, are rather steeply tilted (almost 45° in some places) and dip in a general southward direction. The tilted section exposes somewhat more than 250 feet of strata which include thin marine limestones and shales (up to about 8 feet thick), a few thin coal beds (up to about 1½ feet thick) and some sandstones. The conodonts came from a shale near the bottom of the tilted section.

Later, conodonts were found at a second locality approximately two miles south of Knoxville (NE¼ sec. 24, T. 75. N., R. 20 W., Marion County, Iowa). At that place, black shale which presumably is the same as the black shale of the first locality crops out in a small stream valley, dips about 20° to the north, and contains a few conodonts and some impressions of shark spines. About three feet above this indurated bed, a thin unconsolidated shale provided the other conodonts included in this study. This is assumed to be the same zone that was sampled northwest of Knoxville, for the

stratigraphic position of this shale appears to to be identical with that of the other, and the conodonts are similar.

Pennsylvanian conodonts (particularly those from lower zones) have received little study. Accordingly, the equivalents of the assemblage under consideration are none too clear. The few specimens which are close to or conspecific with species previously described, indicate that the beds from which the present fauna was obtained can perhaps best be correlated with the Cherokee shale (lower Des Moines) of Missouri. However, there are no representatives of the rather easily recognized genus *Gondolella* in the present assemblage. Ellison (1946, fig. 1) has indicated that *Gondolella* is confined to post-Bend (that is, Des Moines and younger) strata. Relatively few conodonts have been described from rocks of Bend age, so that forms of that time are not well known. Also, among conodonts, which are notably facies fossils both as to faunas and portions of faunas, the absence of a given genus is of uncertain significance. Possibly the shale from which this assemblage was secured is pre-Des Moines in age.

Several other types of micro-fossils occur in association with the conodonts at these two localities. Fish spines and plates are particularly abundant. Small high-spired gastropods as well as bryozoan remains are common and a few Foraminifera are present.

We are particularly indebted to Mr. C. B. Campbell of Knoxville, Iowa, whose detailed knowledge of the local geology and the occurrences of the conodonts was a major factor in the success of our collecting trips. Professor A. K. Miller has given us many helpful suggestions during the progress of this study. Through correspondence, Dr. Samuel P. Ellison, Jr. has kindly advised us on several problems. Professor Preston E. Cloud, Jr. criticized the manuscript in completed form. Our illustrations are photographs retouched by Mr. Howard Webster of Iowa City. The specimens have been placed in the repository of the Geology Department at the State University of Iowa. All illustrations are ×40.

SYSTEMATIC PALEONTOLOGY

HIBBARDELLA SUBACODA (Gunnell)

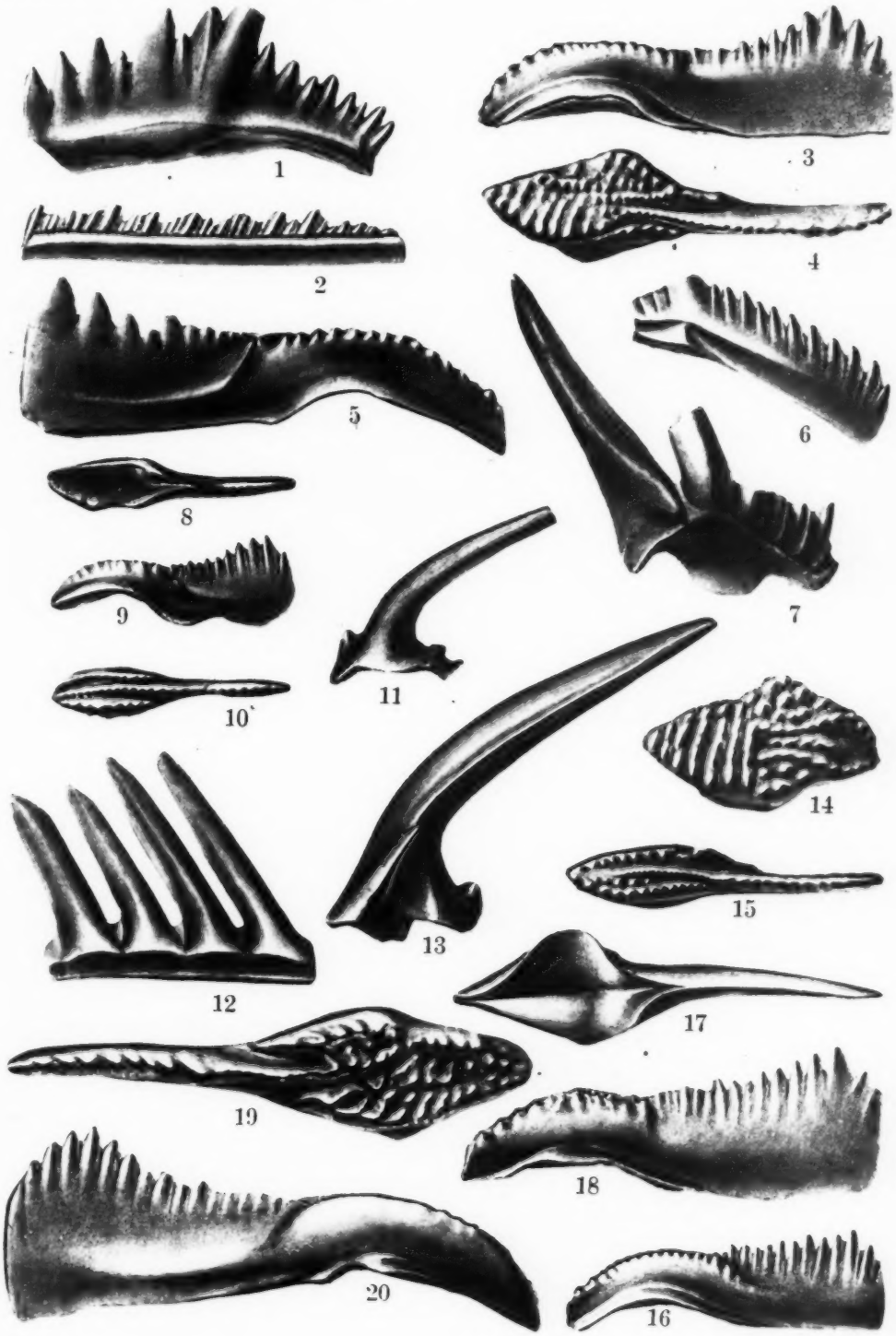
Plate 118, figure 13

Prioniodus subacodus GUNNELL, 1931, Jour. Paleontology, vol. 5, p. 246, pl. 29, fig. 5.
Prioniodus missouriensis GUNNELL, 1931, Jour. Paleontology, vol. 5, p. 247, pl. 29, fig. 9.
Idioprioniodus striatus GUNNELL, 1933, Jour. Paleontology, vol. 5, pp. 264, 265, pl. 32, figs. 36, 37.
Idioprioniodus striatus GUNNELL, 1933, Jour. Paleontology, vol. 5, p. 278.
Hibbardella subacoda ELLISON, 1941, Jour. Paleontology, vol. 15, pp. 108–111, 118, pl. 20, figs. 22, 26.
Hibbardella subacoda ELLISON, 1944, *in* Branson, Missouri Univ. Studies, vol. 19, no. 3, p. 325.

EXPLANATION OF PLATE 118

All illustrated specimens with the exception of figures *2* and *14* are from early Pennsylvanian shale at a locality ¾ mi. northwest of Knoxville, Iowa. Figures *2* and *14* are from the same zone at a locality 2 mi. south of Knoxville. All illustrations are ×40.

FIGS. *1*—*Ozarkodina campbelli* Youngquist and Heezen, n. sp. Outer lateral view of the holotype. (p. 771)
2—*Hindeodella* sp. (p. 769)
3, 4—*Idiognathodus iowaensis* Youngquist and Heezen, n. sp. Lateral and oral views of the holotype. See also figs. *17, 18*. (p. 770)
5—*Idiognathodus attenuatus* Youngquist and Heezen, n. sp. The holotype. (p. 769)
6—*Ozarkodina delicatula* (Stauffer and Plummer). (p. 771)
7—*Metalonchodina deflecta* Youngquist and Heezen, n. sp. The holotype. (p. 771)
8–10—*Streptognathodus delicatulus* Youngquist and Heezen, n. sp. Three views of the holotype. (p. 772)
11—*Ligonodina? abbreviata* Youngquist and Heezen, n. sp. The holotype. (p. 770)
12—*Lonchodus?* sp. (p. 771)
13—*Hibbardella subacoda* (Gunnell). (p. 768)
14—*Idiognathodus* sp. (p. 770)
15, 16—*Streptognathodus symmetricus* Youngquist and Heezen, n. sp. Oral and lateral views of the holotype. (p. 772)
17, 18—*Idiognathodus iowaensis* Youngquist and Heezen, n. sp. Aboral and lateral views of the paratype. See also figs. *3, 4*. (p. 770)
19, 20—*Idiognathodus claviformis* Gunnell. (p. 769)



Youngquist and Heezen, Pennsylvanian conodonts

Our specimen agrees closely with that illustrated by Ellison in 1941 from the Quivera shale of Jackson County, Missouri. The denticles preserved, one on each side of the cusp, are complete and they are strongly compressed, short, and discrete to the base.

Occurrence.—Early Pennsylvanian shale, 3/4 mi. northwest of Knoxville, Iowa. The holotype of this species came from the Fort Scott limestone of the Henrietta group at Lexington, Missouri. Conspecific forms are also reported by Branson (1944, p. 325) to occur in the Cherokee, Pleasanton, Kansas City, Lansing, Douglas and Shawnee groups in Missouri.

Figured Specimen—State Univ. Iowa, 4158.

HINDEODELLA sp.
Plate 118, figure 2

This specimen, although preserving a considerable length of bar, does not retain the cusp, so that specific determination cannot be made with certainty. The bar, however, is pronouncedly rounded in cross section with only a slight aboral flattened zone. The closely appressed denticles are in a somewhat irregular although alternating series—two to four small denticles being intercalated between successive larger ones. When viewed by transmitted light, the denticles do not appear to be "inserted" into the bar, but rather to grade into the deep amber-colored bar material. In all these features our specimen seems close to those from the Dimple limestone of Texas designated as *Hindeodella* sp. by Ellison and Graves, and illustrated by figures 1, 2, and 7 on their plate 1. In addition, our specimen is reminiscent of figures 5 and 12 of *H. irregularis* from the Mineral Wells formation of Texas on Stauffer and Plummer's plate 1.

Occurrence.—Early Pennsylvanian shale, 2 mi. south of Knoxville, Iowa.

Figured Specimen.—State Univ. Iowa, 4159.

IDIOGNATHODUS ATTENUATUS Youngquist and Heezen, n. sp.
Plate 118, figure 5

Platform very narrow in oral view, distinctly longer than blade and only very slightly expanded laterally on the inner side; posterior portion somewhat deflected laterally. Oral ornamentation on anterior third of platform consists of small ridges which radiate obliquely anteriorly from a small carina which extends from the blade a short distance posteriorly on the platform. Posterior two-thirds of platform prominently curved aborally and ornamented by about 12 to 14 transverse ridges. Blade consists of about 8 to 10 denticles; the posterior ones are small, the anterior ones larger in a gradational series. Maximum height of blade is reached at the position of the ultimate anterior denticle. Penultimate and ultimate denticles very large. Aboral third of blade thickened for most of its length, the thickness progressively decreases anteriorly. The very long narrow platform, and its large size serve to distinguish this species from related forms.

Occurrence.—Early Pennsylvanian shale, 3/4 mi. northwest of Knoxville, Iowa.

Holotype.—State Univ. Iowa, 4160.

IDIOGNATHODUS CLAVIFORMIS Gunnell
Plate 118, figures 19, 20

Idiognathodus claviformis GUNNELL, 1931, Jour. Paleontology, vol. 5, pp. 249–250, pl. 29, fig. 21 [not fig. 22].

? Idiognathodus claviformis? STAUFFER and PLUMMER, 1932, Texas Univ. Bull. 3201, pp. 25, 45.

Idiognathodus fustiformis GUNNELL, 1933, Jour. Paleontology, vol. 7, pp. 263, 269–270, pl. 31, fig. 7.

Idiognathodus claviformis ELLISON, 1941, Jour. Paleontology, vol. 15, pp. 108, 109, 111, 135–137, pl. 23, figs. 12–17, 19, 20, 22. [Misprinted as "12, 14–18, 20, 21, 23"].

Idiognathodus claviformis BRANSON and MEHL, 1944, *in* Shimer and Shrock, Index fossils of North America, p. 246.

Idiognathodus claviformis ELLISON, 1944, *in* Branson, Missouri Univ. Studies, vol. 19, no. 3, p. 325.

Representatives of this species are large, with the platform somewhat oval in oral outline. Maximum width of platform attained slightly anterior to midlength. Blade slightly sinuous in oral view, stout, and moderately sharp aborally. Maximum oral-adoral dimension attained in anterior third of blade. About 15 to 17 denticles which are subequal in size compose the blade. Platform irregularly rugose with margins slightly higher than central zone. Of the several specimens which have been referred to this somewhat broadly interpreted species, the genotype of

Idiognathodus, our specimen appears closest to that illustrated by Gunnell (1933, pl. 31, fig. 7) from the "Cherokee shale, overlying Lexington coal, Lexington, Missouri."

Occurrence.—Early Pennsylvanian shale, 3/4 mi. northwest of Knoxville, Iowa. Stated by Branson (1944, p. 325) to occur in the Cherokee, Henrietta, Pleasanton, and Kansas City groups in Missouri. May also occur in the Mineral Wells formation of Texas.

Figured Specimen.—State Univ. Iowa, 4161.

IDIOGNATHODUS IOWAENSIS Youngquist and Heezen, n. sp.
Plate 118, figures 3, 4, 17, 18

? Idiognathodus sp. BAILEY, *in* Branson, Missouri Univ. Studies, vol. 19, no. 3, p. 305, pl. 44, figs. 26–28.

Outline of platform in oral view asymmetrically lanceolate. Inner posterior margin of plate essentially straight; outer posterior margin broadly rounded. The extension of the blade posteriorly on to the platform as a short carina is bordered on each side by a small short groove or sulcus. Inner side of platform somewhat expanded laterally to form a nodose lobe, posterior outer portion has five or six moderately distinct transverse ridges formed by closely spaced nodes. Blade slightly bowed, platform of specimen moderately arched. The 12 to 16 denticles composing the blade attain their greatest size near (but not at) the anterior end of the specimen. Two or three smaller denticles occur anterior of the largest denticle of the blade. As shown by figure 17, the aboral margins of the platform are broadly flared to encompass a large escutcheon or excavation which persists in progressively narrowed form anteriorly for a short distance on to the blade. The remainder of the blade is sharp aborally.

This species is perhaps closest to *I. magnificus* Stauffer and Plummer, but can be distinguished from that form in the possession of only one, rather than two, nodose lobe-like lateral expansions of the anterior portion of the platform. The specimens from the "Lower Pennsylvanian" of Missouri illustrated by figures 26–28 on plate 44 in Branson (1944) may be referable to our species.

Occurrence—Early Pennsylvanian shale, 3/4 mi. northwest of Knoxville, Iowa.

Types.—State Univ. Iowa, 4162 (holotype, figs. 3, 4), 4163 (paratype, figs. 17, 18).

IDIOGNATHODUS sp.
Plate 118, figure 14

The platform is entire but essentially all of the blade is missing from this specimen. Oral ornamentation of the platform consists of three longitudinal nodose ridges extending from the anterior end of the plate posterior to midlength (presumably the median ridge is the posterior extension of the blade). On either side of the ridges are small sublenticular areas with nodose ornamentation; the inner of these two areas is the larger. The posterior half of the plate is transversely rugose from the outer side almost to (but not quite) the inner side. These ridges consist of closely spaced partially fused nodes.

Although incomplete, this specimen is close to the individuals illustrated from the Cherokee shale in Missouri by Ellison (1941, pl. 23, figs. 2, 3,—misprinted as "2, 4") and referred to *I. magnificus*.

Occurrence.—Early Pennsylvanian shale, 2 mi. south of Knoxville, Iowa.

Figured Specimen.—State Univ. Iowa, 4164.

LIGONODINA? ABBREVIATA Youngquist and Heezen, n. sp.
Plate 118, figure 11

Cusp slender, strongly curved posteriorly, rounded on outer (figured) side, flattened on inner side, sharp laterally, deeply and narrowly excavated aborally. Anticusp short, deflected laterally, bearing about two or three small denticles. Bar very short, possessing a few short denticles. Specimen rounded on outer aboral margin, flattened on inner side.

Lack of symmetry and absence of a third bar limb exclude this form from the genus *Hibbardella* with which it is found. Although the bar is very short, the posteriorly curved cusp together with the laterally deflected denticulate anticusp indicate that this specimen is most probably referable to *Ligonodina*. No very similar species is known.

Occurrence.—Early Pennsylvanian shale, 3/4 mi. northwest of Knoxville, Iowa.

Holotype.—State Univ. Iowa, 4165.

LONCHODUS? sp.
Plate 118, figure 12

Denticles parallel, inclined uniformly posteriorly, and not curved inward appreciably. A slight lateral compression of the denticles gives them an elliptical cross section—they have sharp edges anterior-posteriorly. Denticles are discrete to the place of junction with the bar except for a small web-like structure between adjacent denticles near their bases.

The specimen described from the Mineral Wells formation of Texas by Stauffer and Plummer as *Lonchodus simplex* (?) Pander and illustrated by their figure 1 of plate 2 is strikingly similar to our individual in essentially every detail. In addition to commenting on the "web near the base," Stauffer and Plummer (1932, p. 38) state that the "bar appears to be formed by a fusing of the bases of the teeth. . . . " This description is equally apt for our specimen and it seems likely that the two may be conspecific, although their reference to Pander's species is of doubtful value.

Occurrence.—Early Pennsylvanian shale, 3/4 mi. northwest of Knoxville, Iowa.

Figured Specimen.—State Univ. Iowa, 4166.

METALONCHODINA DEFLECTA Youngquist and Heezen, n. sp.
Plate 118, figure 7

Cusp, anterior-most denticle and adjacent portion of bar deflected inward. All denticles and cusp incline anteriorly and inward. The cusp is sharp anterior-posteriorly, has a small anticusp anteriorly, and is slender and suboval in cross section. Denticles are about six in number, are large (except for posterior two) and more rounded than the cusp. Aborally, and slightly anterior of midlength the bar bears a flange-like extension. In view of the statement by Ellison (1941, p. 116) "that the attachment scar is commonly beneath one of the longer denticles" rather than the cusp, this aboral flange on our specimen presumably represents part of the zone of attachment.

Occurrence.—Early Pennsylvanian shale, 3/4 mi. northwest of Knoxville, Iowa.

Holotype.—State Univ. Iowa, 4167.

OZARKODINA CAMPBELLI Youngquist and Heezen, n. sp.
Plate 118, figure 1

Denticles unequal in size, those anterior to the cusp being much the larger. The portion of the blade anterior to the cusp is also much larger than the posterior part but each section has approximately an equal number of denticles—seven or eight. Although the denticles located near the extremities of the blade are, in general, smaller than those nearer the cusp, the denticle arrangement is irregular to the extent that no gradational series exists. The denticles are partially sheathed by the blade and much compressed laterally. The aboral margin of the blade is somewhat expanded laterally to form ridge-like processes both on the inner and outer sides in a manner somewhat reminiscent of typical *Bryantodus*, which, however, is commonly regarded as restricted to the Devonian and Mississippian. Aborally, the blade is narrowly grooved near its midlength and somewhat flattened anteriorly. This escutcheon persists only a short distance posterior to the cusp.

This form is distinguished from other species of *Ozarkodina* such as *O. delicatula* in the possession of coarser, larger and more irregularly developed denticles. The species is named in recognition of the work of Mr. C. B. Campbell, enthusiastic collector of Pennsylvanian conodonts in Iowa.

Occurrence.—Early Pennsylvanian shale, 3/4 mi. northwest of Knoxville, Iowa.

Holotype.—State Univ. Iowa, 4168.

OZARKODINA DELICATULA (Stauffer and Plummer)
Plate 118, figure 6

Bryantodus delicatulus STAUFFER and PLUMMER, 1932, Texas Univ. Bull., no. 3201, p. 29, pl. 2, fig. 27.

Bryantodus nasutus STAUFFER and PLUMMER, 1932, Texas Univ. Bull., no. 3201, p. 29, pl. 2, fig. 28.

Bryantodus sulcatus STAUFFER and PLUMMER, 1932, Texas Univ. Bull., no. 3201, p. 30, pl. 2, figs. 11, 14, 30.

Bryantodus delicatus GUNNELL, 1933, Jour. Paleontology, vol. 7, pp. 264, 267–268, pl. 32, fig. 43.

Bryantodus rugosus GUNNELL, 1933, Jour. Paleontology, vol. 7, pp. 264, 268, pl. 32, fig. 44.

Bryantodus strigatus GUNNELL, 1933, Jour. Paleontology, vol. 7, pp. 264, 268, pl. 32, fig. 45.

Bryantodus strigillatus GUNNELL, 1933, Jour. Paleontology, vol. 7, pp. 264, 268, pl. 32, fig. 46.
Ozarkodina delicatula ELLISON, 1941, Jour. Paleontology, vol. 15, pp. 108, 109, 110, 111, 120, pl. 20, figs. 40–42, 47.
Ozarkodina delicatula ELLISON and GRAVES, 1941, Missouri Univ. Sch. Mines and Metall. Bull. tech. ser., vol. 14, no. 3, pp. 3, 4, pl. 1, figs. 12–14.
Ozarkodina delicatula BRANSON, 1944, Missouri Univ. Studies, vol. 19, no. 3, p. 327.

Specimen gently bowed and strongly arched. Blade thin. Greater portion of blade posterior to the cusp is missing; the blade anterior to the cusp is entirely complete, however, and preserves 11 denticles which are subequal in size, partially confluent and all curved slightly posteriorly. Escutcheon beneath cusp is small and encompassed by flange-like expansions of the aboral margin of the blade.

This species seems to have been broadly interpreted as the specimens which have been referred to it show a variety of forms, anterior and/or posterior to the cusp, chiefly in the number of denticles which vary from about 9 (*Bryantodus delicatus* Gunnell) to about 17 or 18 (*Ozarkodina delicatula* Ellison, 1941, pl. 20, fig. 42). Of the specimens which have been referred to this species, ours is perhaps closest to the particular individual illustrated by Ellison (1941, pl. 20, fig. 40) which came from the Hushpunckney shale in Missouri.

Occurrence.—Widely distributed. Known from formations ranging in age from Lower Pennsylvanian (Cherokee shale) to Lower Permian? (Big Blue series). Our specimen came from an early Pennsylvanian shale, 3/4 mi. northwest of Knoxville, Iowa.

Figured Specimen.—State Univ. Iowa, 4169.

STREPTOGNATHODUS DELICATULUS Youngquist and Heezen, n. sp.
Plate 118, figures 8–10

Blade and platform narrow, blade slightly the longer and consists of about 10 to 12 laterally compressed denticles. It attains maximum size at the anterior penultimate denticle. Aborally, the blade margin (slightly broken) is moderately sharp. Maximum thickness of blade is attained slightly aborad of median. Platform is narrow, concave on its oral surface, divided into two subequal longitudinal zones by a small carina extending from the blade to the posterior end of the specimen. In profile, platform is arched. Aborally, the margins of the platform are flared to a moderate degree around an elongate, deep escutcheon.

In lateral view, this specimen superficially resembles the forms illustrated by Stauffer and Plummer as *Idiognathodus delicatus* Gunnell. However, the distinct longitudinal (rather than transverse) orientation of the major and minor features of the oral platform surface clearly serve to distinguish our form generically from *Idiognathodus.*

Occurrence.—Early Pensylvanian shale, 3/4 mi. northwest of Knoxville, Iowa.

Holotype.—State Univ. Iowa, 4170.

STREPTOGNATHODUS SYMMETRICUS Youngquist and Heezen, n. sp.
Plate 118, figures 15, 16

Platform almost bilaterally symmetrical, divided medianly by a low, finely nodose carina which extends from the blade in diminishing distinctness onto the posterior third of the platform where it disappears. Blade and platform subequal in length. In profile, aboral margin of blade is essentially straight and it is anteriorly terminated at nearly a right angle. About 10 to 13 denticles which are subequal in size constitute the blade. The greatest oral-aboral dimension of the blade is attained at the penultimate or antepenultimate denticle. The posterior portion of the platform is curved aborally; the entire platform is gently arched. The blade, but not the platform is slightly bowed. Escutcheon deep, narrow,

This species is similar to *S. delicatulus* with which it is associated. However, it differs from that form in the profile of the blade, the length of the blade relative to the platform, the lack of a carina the entire length of the platform and the more nearly symmetrical oral outline of the platform.

Occurrence.—Early Pennsylvanian shale, 3/4 mi. northwest of Knoxville, Iowa.

Holotype.—State Univ. Iowa, 4171.

REFERENCES

BRANSON, E. B., and MEHL, M. G., 1944, *in* Shimer, H. W., and Shrock, R. R., Index fossils of North America, pp. 235–246, pls. 93, 94.
BRANSON, E. B., 1944, The geology of Missouri:

Missouri Univ. Studies, vol. 19, no. 3, pp. 1–535, pls. 1–49.

COOPER, C. L., 1947, Role of microfossils in interregional Pennsylvanian correlations: Jour. Geology, vol. 55, pp. 261–270.

ELLISON, SAMUEL P., JR., 1941, Revision of the Pennsylvanian conodonts: Jour. Paleontology, vol. 15, pp. 107–143, pls. 20–23.

——, and GRAVES, R. W., JR., 1941, Lower Pennsylvanian (Dimple limestone) conodonts of the Marathon region, Texas: Missouri Univ. Sch. Mines and Metallurgy Bull., tech. ser., vol. 14, no. 3, pp. 1–21, pls. 1–3.

——, 1946, Conodonts as Paleozoic guide fossils: Am. Assoc. Petrol. Geol., Bull., vol. 30, pp. 93–110.

GUNNELL, F. H., 1931, Conodonts from the Ft. Scott limestone of Missouri: Jour. Paleontology, vol. 5, pp. 244–255, pl. 29.

——, 1933, Conodonts and fish remains from the Cherokee, Kansas City, and Wabaunsee groups of Missouri and Kansas: Jour. Paleontology, vol. 7, pp. 261–297, pls. 31–33.

HARRIS, R. W., and HOLLINGSWORTH, R. V., 1933, New Pennsylvanian conodonts from Oklahoma: Am. Jour. Sci., 5th ser., vol. 25, pp. 193–204, 1 pl.

STAUFFER, C. R., and PLUMMER, H. J., 1932, Texas Pennsylvanian conodonts and their stratigraphic relations: Texas Univ. Bull., no 3201, pp. 13–50, pls. 1–4.

JOURNAL OF PALEONTOLOGY, VOL. 22, NO. 6, PP. 774–782, PL. 119, NOVEMBER 1948

FORAMINIFERA FROM THE MIOCENE ASTORIA FORMATION IN SOUTHWESTERN WASHINGTON

WELDON W. RAU
The State University of Iowa, Iowa City, Iowa

ABSTRACT—A small but significant foraminiferal fauna from the Astoria formation in Grays Harbor County, Washington, is described and illustrated. The assemblage is indicative of a cool to temperate marine environment of intermediate depth. An age of lower to middle Miocene is indicated by the fauna and there is some evidence suggesting that it is upper lower Miocene (upper Saucesian).

INTRODUCTION

EXTENSIVE Tertiary marine deposits are present in southwestern Washington. Many of these beds have been assigned to the Miocene, and are now considered equivalent to part of the type Astoria formation at Astoria, Oregon. Several authors formerly believed these strata to be Oligocene in age. However, later studies of Dall, Clark, Tegland, Howe, Stewart, Etherington, and Weaver (Weaver, 1937, p. 175), have shown that the beds are definitely Miocene.

Previous studies of age determination and correlation were based almost entirely on megafossils. The presence of numerous foraminiferal species has been reported by several workers, but in so far as the author has been able to ascertain, none have been described from the Astoria of southwestern Washington. Foraminifera are, however, recorded from the type locality of the Astoria formation in Oregon and also from the underlying Blakely formation (upper Oligocene or lower Miocene) of Washington (Kleinpell, 1938). In the present paper, Foraminifera from the Astoria formation of southwestern Washington are illustrated and described and their significance is discussed. The material was collected by the author, during the summer of 1946, from a new road cut about 50 feet high in the SE ¼ NW ¼ sec. 28, T. 17 N., R. 8 W., Montesano Quadrangle U. S. Army Engineers. Seven samples were taken at equal stratigraphic intervals. The material, a bluish-gray, fine-grained, tuffaceous, very slightly indurated shale, is representative of the shaley phase of the Astoria. Several species of mollusks, some ostracodes, and a few sponge spicules were found in association with the Foraminifera.

COMPOSITION OF FAUNA

Although numerous specimens of Foraminifera occur in the material, there are only 11 species contained in 11 genera of 7 families. Four forms are identified as previously described species, three are new species, and four are not definitely classified as the specimens are either too incomplete or not well enough preserved to permit classification. *Cassidulina pulchella* d'Orbigny is by far the most common species. It, together with *Nonion costiferum* (Cushman), *Bulimina oiula* d'Orbigny, and new species belonging in the genera *Bolivina*, *Uvigerina*, and *Baggina* constitute the bulk of the fauna. The remaining five species are present in such small numbers that they may not be indigenous in the fauna.

ENVIRONMENTAL CONDITIONS

The fine-grain nature of the sediments and the absence of abundant carbonaceous material suggest that deposition took place at a moderate depth some distance from the shoreline. Etherington (1931, p. 42) points out that the Astoria in the Grays Harbor area grades from sandstones with occasional lignite seams in the east into thick beds of shale to the west, a gradation typical of a westward-deepening sea.

The Foraminifera support the evidence of at least intermediate depth of deposition. Most significant is the extreme abundance of *Cassidulina*, a cold-water genus occurring in intermediate to deep water. *Pulvinulinella* although not common in the fauna, is a temperate-to-cold water form known from considerable depths. *Lagena*, represented by only one specimen, is a cool-to-cold-water genus which may occur at all depths. How-

ever, *Baggina*, which is represented by a substantial number of specimens, is generally considered a shallow-water genus; its presence suggests that the depth was not extreme, but perhaps intermediate or shallow enough to allow this form to exist somewhat successfully.

The presence of *Quinqueloculina* is significant. It is known as a warm-water genus found at shallow to medium depths. It is, of course, possible that representatives of this genus were brought in from another environment. Their extremely thick tests are almost always broken and show definite signs of wear, suggesting (especially when compared to the excellent preservation of delicate forms such as *Bulimina*) that they had undergone considerable transportation. Also, they may, of course, be representatives of an older fauna which has been reworked and deposited with the present material. The remaining genera of the fauna are all known from widely varied environments in both depth and temperature. Nevertheless, it would seem that they were deposited in a cool to temperate sea at an intermediate depth some distance from the shoreline, a conclusion in harmony with the preponderance of the more significant foraminiferal evidence as well as the nature of the sediments.

AGE AND CORRELATION

Although the fauna is small, it is nevertheless indicative of the age of the containing beds. The geologic range of several genera contained in the assemblage suggests that the sediments are not older than Miocene. *Cassidulina*, the most common genus in the fauna, is known to have existed from the Cretaceous to the Recent, but it occurs largely in the Miocene and younger strata. *Uvigerina* ranges from Eocene to Recent but is most common in the Miocene; it ranks second in abundance in the fauna. *Pulvinulinella*, although not represented by a large number of specimens, is quite significant in that in California it has been reported from only the Miocene. However, in other regions it occurs in sediments as old as Cretaceous. The remaining genera of the fauna are known to range throughout the Tertiary and they are, therefore, not very helpful in determining the precise age of the containing beds. Nevertheless, the assemblage as a whole shows a marked evolutionary advance over the Eocene and Oligocene foraminiferal faunas of the same general area (see Beck, 1943: Rau, 1948). There is a complete absence of *Robulus*, a genus very common in the Lower Tertiary of southwestern Washington. On the other hand, such genera as *Baggina*, *Uvigerina*, *Pulvinulinella*, and *Bolivina*, all of which are represented at least substantially well in the present fauna, are entirely absent or at best very meagerly represented in subjacent beds of the Lower Tertiary. The geologic range of previously described species, *Cassidulina pulchella*, *Bulimina ovula*, *Nonion costiferum* and *Pulvinulinella parva*, is indeed significant. They are all known from the lower Miocene of California. However, *P. parva* is not recorded as occurring above the lower Miocene and *N. costiferum* above the middle Miocene. Moreover, *C. pulchella* extends only into the lowermost part of the upper Miocene (lower Mohnian). Furthermore, although these four species are all known from some part of the lower Miocene of California, they occur together only in the uppermost part of the lower Miocene, the upper Saucesian (Kleinpell, 1938). The foraminiferal evidence then, though not entirely conclusive, is suggestive of an upper lower Miocene (upper Saucesian) age for the containing beds, and can be said to indicate that these strata are of lower to middle Miocene age.

A satisfactory correlation of the Astoria formation in the Grays Harbor area on the basis of the present fauna with beds in other regions is almost impossible. As previously noted, the assemblage is relatively small. Moreover, the nearest beds with which correlation could be made are those of California. These are at a considerable distance and almost certainly were deposited under somewhat different environmental conditions. However, it is worth noting that a foraminiferal assemblage from the Temblor of the San Joaquin basin (Cushman and Parker, 1931) contains all the genera of the present Astoria fauna with the exception of *Quinqueloculina* and *Uvigerina*. As mentioned previously, *Quinqueloculina* is probably not indigenous in the present Astoria material. Although *Uvigerina is* absent

in Temblor fauna, *Uvigerinella*, a very closely related form, is present. Also, an assemblage from Los Sauces Creek in the Ventura basin of California (Cushman and Laiming, 1931) contains all the Astoria genera with the exception of *Baggina* and those not known in Cushman and Parker's assemblage.

In summary, the Foraminifera of the Astoria formation in the Grays Harbor area indicate a lower to middle Miocene age for the containing beds, and there is some evidence to support the more specific age of upper lower Miocene (upper Saucesian). Foraminiferal assemblages known from the Temblor of California show considerable similarity to the present Astoria fauna.

ACKNOWLEDGMENTS

The author wishes to express his gratitude to Dr. A. K. Miller for many helpful suggestions and continual encouragement rendered throughout the preparation of this report. Acknowledgment is due, also, to Dr. R. L. Lupher for suggesting the collecting area, and to Mr. Howard Webster who retouched all the photographs accompanying this paper.

SYSTEMATIC DESCRIPTIONS

Family MILIOLIDAE

Genus QUINQUELOCULINA d'Orbigny, 1826

QUINQUELOCULINA sp.

Plate 119, figures 1–3

Description.—Test of medium size, length considerably greater than width, slightly broader than thick, periphery broadly rounded, last formed chamber truncated with apertural face bent back forming an angle slightly less than 90 degrees with the periphery; chambers distinct, inflated, last formed chamber strongly curved at end opposite aperture, constituting the entire peripheral area at that end; sutures distinct, depressed; walls porcellaneous, thick; aperture circular with a small modified bifid tooth projecting from a somewhat flattened base.

Length, 0.76 mm., breadth, 0.49 mm.; thickness, 0.42 mm.

Remarks.—This form, although the most sturdy one in the assemblage, is almost always found as fragments. Even the figured specimen, which is the only complete one in the collection, shows signs of abrasion. This fact suggests that it underwent considerable transportation before it was finally deposited. Possibly it was originally deposited in older sediments which were later reworked.

No species are known from the area under consideration that are particularly close to this form. *Q. weaveri* Rau of the Porter shale of the Lincoln formation is similar insofar as size and shape are concerned, but it differs in that the chambers are depressed and the aperture is devoid of any dentition.

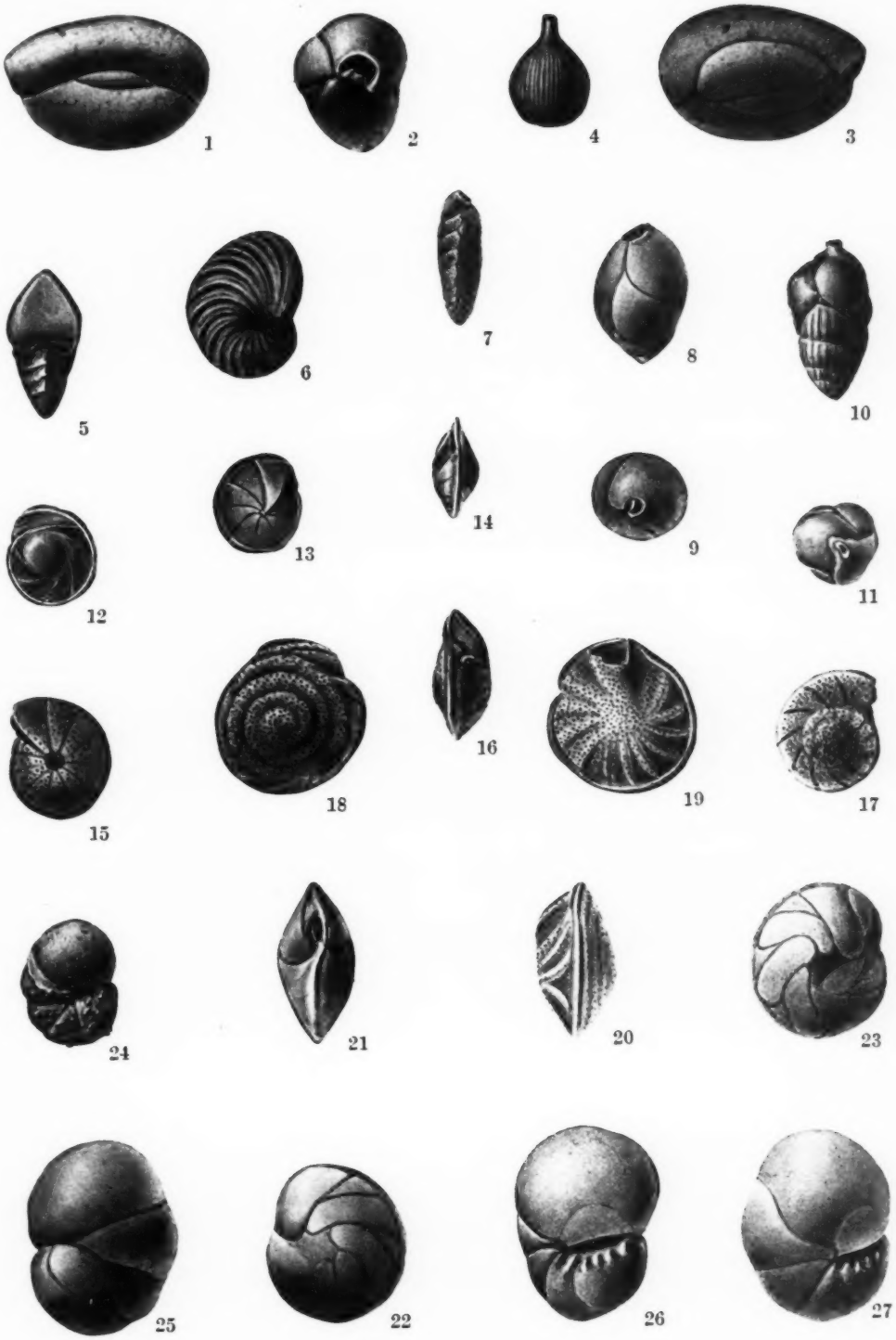
Occurrence.—Astoria formation in a new road cut adjacent to state highway 9, some 2 miles northeast of the junction of U. S. highway 101 and state highway 9, Grays Harbor County, Washington. Most of the specimens obtained came from the upper portion of the road cut.

Figured specimen.—State Univ. Iowa, 6778.

EXPLANATION OF PLATE 119

All specimens illustrated are from the Astoria formation exposed in a new road cut adjacent to state highway 9, some 2 miles northeast of the junction of U. S. Highway 101 and State Highway 9, Grays Harbor County, Washington. The figures are ×40.

FIGS. *1, 2, 3*—*Quinqueloculina* sp. (p. 776)
4, *Lagena* sp. (p. 777)
5, 6—*Nonion costiferum* (Cushman) (p. 777)
7—*Bolivina astoriensis*, n. sp. (p. 778)
8, 9—*Bulimina ovula* d'Orbigny (p. 777)
10, 11—*Uvigerina montesanensis*, n. sp. (p. 778)
12–14—*Pulvinulinella parva* Cushman and Laiming (p. 780)
15–17—*Cibicides* aff. *C. perlucida* Nuttall (p. 781)
18–20—*Eponides?* sp. (p. 779)
21–23—*Cassidulina pulchella* d'Orbigny (p. 780)
24–27—*Baggina washingtonensis*, n. sp., *24*, highly ornamented form (p. 779)



Rau, Miocene Foraminifera

Family LAGENIDAE
Genus LAGENA Walker and Jacob, 1798
LAGENA sp.
Plate 119, figure 4

Description.—Test small, globular; chamber very slightly longer than broad, somewhat more acute near the neck than at the base; walls very finely perforate and ornamented with numerous low-lying, fine, longitudinal costae, occasionally extending up onto the neck; a very small almost obscure spine at the base; aperture small but a distinct round opening at the end of a long unlipped neck.

Length, 0.38 mm.; diameter, 0.28 mm.

Remarks.—One essentially perfect specimen occurs in samples of this study. It is similar to *L. substriata* in that it is ornamented with numerous fine costae but differs in that the chamber is broader and the angle made by the neck and the chamber is considerably less. The present form is also similar to several specimens figured as *Lagena strumosa* Reuss (Kleinpell, 1938, p. 226, pl. 4, fig. 16; Galloway and Morrey, 1929, p. 20, pl. 2, fig. 8) in that the test is much the same shape and the costae are fine and numerous, but the spine is not as prominent. The present form varies considerably from the holotype of *L. strumosa* Reuss. Since only one specimen is available for study at this time it seems best to withhold specific identification.

Occurrence.—Astoria formation in a new road cut adjacent to state highway 9, some 2 miles northeast of the junction of U. S. highway 101 and state highway 9, Grays Harbor County, Washington.

Figured specimen.—State Univ. Iowa, 6779.

Family NONIONIDAE
Genus NONION Montfort, 1808
NONION COSTIFERUM (Cushman)
Plate 119, figures 5, 6

Nonionina boueana CHAPMAN, 1900, California Acad. Sci. Proc. Geol., vol. 1, p. 255, pl. 30, figs. 14, 14a.

Nonionina costifera CUSHMAN, 1926, Cushman Lab. Foram. Research Contr., vol. 1, pt. 4, p. 90, pl. 13, figs. 2a–c.—MACARTHUR, 1927, Micropaleo. Bull., vol. 1, no. 5, p. 74.

Nonion costifera (Cushman) CUSHMAN, STEWART, and STEWART, 1930, San Diego Soc. Nat. History Trans., vol. 6, no. 2.—CUSHMAN and LAIMING, 1931, Jour. Paleontology, vol. 5, p. 104, pl. 11, figs. 9a, b.—HUGHES and LAIMING, 1931, *in* Hoots, U. S. Geol. Survey Prof. Paper 165-C, p. 99—DORN, 1932, Micropaleo. Bull., vol. 3, no. 2, p. 29.—SNEDDEN, 1932, Micropaleo. Bull., vol. 3, no. 2, pp. 43, 45.

Nonion costiferum (Cushman) CUSHMAN and PARKER, 1931, Cushman Lab. Foram. Research Contr., vol. 7, pt. 1, p. 7, pl. 1, figs. 27a, b.—CUSHMAN and BARBAT, 1932, Cushman Lab. Foram. Research Contr., vol. 8, pt. 2, pp. 32, 40.—GOUDKOFF, 1934, Am. Assoc. Petroleum Geologists Bull., vol. 18, no. 4, p. 456.—KLEINPELL *in* Packard and Kellogg, 1934, Carnegie Inst., Wash., Publ. no. 447, Contr. Paleontology, pp. 17, 18.—WOODRING, BRAMLETTE, and KLEINPELL, 1936, Am. Assoc. Petroleum Geologists Bull., vol. 20, no. 2, p. 136.—KLEINPELL, 1938, Miocene Stratigraphy of California, *published by* Am. Assoc Petroleum Geologists, p. 229, pl. 15, figs. 13a, b.

Dimensions.—Average length, 0.80 mm.; breadth, 0.60 mm.; thickness, 0.40 mm.

Remarks.—This species is rather common in the present material. The figured specimen is smaller than most in the collection presumably because it is in an early mature stage of development. It is figured because the raised, limbate sutures and the heart-shaped apertural face, which typify this species, are best shown on it.

Occurrence.—Astoria formation in a new road cut adjacent to state highway 9, some 2 miles northeast of the junction of U. S. highway 101 and state highway 9, Grays Harbor County, Washington. It has been recorded previously from numerous areas of the lower and middle Miocene of California and Oregon (see Kleinpell, 1938, pp. 229–231, for specific localities).

Figured specimen.—State Univ. Iowa, 6780.

Family BULIMINIDAE
Genus BULIMINA d'Orbigny, 1826
BULIMINA OVULA d'Orbigny
Plate 119, figures 8, 9

Bulimina ovula D'ORBIGNY, 1839, Voy. Amer. Merid., vol. 5, pt. 5, p. 51, pl. 1, figs. 10, 11.—CUSHMAN, 1926, Cushman Lab. Foram. Research Contr., vol. 2, pt. 3, p. 55, pl. 7, fig. 2;—, 1927, Bull. Scripps Instit. Oceanography, Tech. Ser., vol. 1, p. 150, pl. 2, fig. 10; CUSHMAN and MOYER, 1930, Cushman Lab. Foram. Research Contr., vol. 6, pt. 3, p. 56, pl. 7, fig 21; WOODRING, BRAMLETTE, and KLEINPELL, 1936, Am. Assoc. Petroleum Geologists Bull., vol. 20, no. 2, p. 144; CUSHMAN and LEROY, 1938, Jour. Paleontology, vol. 12, p. 125, pl. 22, figs. 18a, b; KLEINPELL, 1938, Miocene Stratigraphy of California, *published by* Am.

Assoc. Petroleum Geologists, pp. 256, 257, pl. 7, fig. 2; CUSHMAN and PARKER, 1940, Cushman Lab. Foram. Research Contr., vol. 16, pt. 1, pp. 10, 11, pl. 2, figs. 13–15.

Dimensions.—Average length, 0.50 mm.; diameter, 0.40 mm.

Remarks.—This form, which is common in the collection under consideration, shows considerable variation in shape as do the previously figured specimens of this species. Such a variation is probably due to trimorphism. Those with a blunt initial end possibly represent a megalospheric variation whereas the pointed types such as the figured specimen are perhaps microspheric forms. All specimens have a large, elongate aperture with a distinct dentition, which projects slightly above the major portion of the test.

Occurrence.—Astoria formation in a new road cut adjacent to state highway 9, some 2 miles northeast of the junction of U. S. highway 101 and state highway 9, Grays Harbor County, Washington. Recorded previously from lower to upper Miocene in California (see Kleinpell, 1938, pp. 256, 257, for some specific localities) and at a depth of some 400 fathoms in Recent deposits off the California coast. Type specimens came from the coast of Chile and Peru.

Figured specimen.—State Univ. Iowa, 6781

Genus BOLIVINA d'Orbigny, 1839
BOLIVINA ASTORIENSIS Rau, n. sp.
Plate 119, figure 7

Description.—Test small, elongate, somewhat compressed, slightly twisted, tapering rapidly in early stage, very gradually in later development, greatest breadth near apertural end, periphery subacute; chambers distinct, numerous, early ones very low, increasing rapidly in height, last 5 pairs making up three-fourths the test, 10 to 12 pairs in all, practically no overlapping, forming a nearly straight medial line, last formed chamber very slightly inflated; sutures practically straight, approaching the periphery somewhat obliquely, only very slightly depressed beneath last formed chamber, the remaining ones flush with the surface, more or less limbate throughout; walls thin, hyaline, finely perforate; aperture a relatively large elongate opening situated subterminally on the last formed chamber, no apparent dentition.

Length, 0.52 mm.; breadth, 0.17 mm.; thickness, 0.09 mm.

Remarks.—This small species is found throughout the present material and is especially common in samples from the upper part of the road cut. It seems most similar to *Bolivina pseudospissa* Kleinpell, described and illustrated from the upper Miocene of California, but differs in that the walls are hyaline throughout with no color distinction between the central part of the chambers and the areas adjacent to the sutures; the test is slightly but distinctly twisted; and the aperture is definitely subterminal rather than terminal as in *B. pseudospissa*. *Bolivina advena* Cushman superficially resembles this species in that the shape of the test and the arrangement of the chambers are somewhat similar. However, in the present form, the early portion of the test is not compressed more than the rest, the early sutures do not display more limbation than the later ones, and the test is slightly twisted. The relatively large aperture together with the arrangement of the chambers and the general shape of the test is a unique combination which typifies this species.

Occurrence.—Astoria formation in a new road cut adjacent to state highway 9, some 2 miles northeast of the junction of U. S. highway 101 and state highway 9, Grays Harbor County, Washington.

Holotype.—State Univ. Iowa, 6782.

Genus UVIGERINA d'Orbigny, 1826
UVIGERINA MONTESANENSIS Rau, n. sp.
Plate 119, figures 10, 11

Description.—Test elongate, nearly twice as long as broad, greatest breadth near the apertural end, tapering rapidly in early stage, very gradually in later development, more or less triangular in cross section; chambers distinct, inflated, especially those of the last formed whorl, triserially arranged throughout, 5 whorls in all; sutures distinct, depressed, considerably so in last formed whorl; walls thin, finely perforate, ornamented with low rather widely spaced longitudinal costae, most pronounced on the early portion, continuous over adjacent chambers, last 1 or 2 chambers without

costae; aperture more or less elliptical on a short very slightly lipped neck.

Length, 0.60 mm.; breadth, 0.35 mm.

Remarks.—This form is the second most abundant species in the material being studied. It is quite similar to *Uvigerina segundoensis* Cushman and Galliher from the upper Miocene of California in that the chamber arrangement and apertural features are similar. The present form differs, however, in that the test is somewhat triangular in cross section; its greatest breadth is farther removed from the central part of the test; and the costae are continuous over adjacent chambers. *Uvigerina subperegrina* Cushman and Kleinpell, known from the upper Miocene of both California and the East Coast, has a general appearance similar to that of the present form but differs in that the test is depressed, and the costae are not continuous over the adjacent chambers.

Some variation from the typical form is displayed in other specimens of the group under consideration. A number are some what narrower with respect to their length. Others show varying degrees of ornamentation, either with more or less distinct costae than the type. However, all specimens have the fundamental characteristics of the typical form.

Occurrence.—Astoria formation in a new road cut adjacent to state highway 9, some 2 miles northeast of the junction of U. S. highway 101 and state highway 9, Grays Harbor County, Washington.

Holotype.—State Univ. Iowa, 6783.

Family ROTALIIDAE
Genus EPONIDES Montfort, 1808
EPONIDES ? sp.
Plate 119, figures 18–20

Description.—Test nearly equally biconvex, periphery with a short thick keel, nonumbilicate; chambers indistinct, numerous, approximately 13 in last formed whorl, 5 whorls visible on dorsal side, only last formed one on ventral side; sutures distinct ventrally, decidedly raised and limbate near periphery, strongly oblique dorsally, most distinct between whorls; surface coarsely perforate; aperture obscure.

Diameter, 0.60 mm.; thickness, 0.35 mm.

Remarks.—Only a few incomplete and poorly preserved specimens of this form are available for study. They seem to be best referred to the genus *Eponides*. However, the aperture is indistinguishable in all the specimens. Therefore, it is not possible to be certain of their generic affinities. So far as determinable, this form is without close similarity to any previously recorded *Eponides*. It is described and illustrated here as it may be of some importance in future work.

Occurrence.—Astoria formation in a new road cut adjacent to state highway 9, some 2 miles northeast of the junction of U. S. highway 101 and state highway 9, Grays Harbor County, Washington.

Figured Specimen.—State Univ. Iowa, 6784.

Genus BAGGINA Cushman, 1926
BAGGINA WASHINGTONENSIS Rau, n. sp.
Plate 119, figures 24–27

Description.—Test trochoid, subglobular, periphery broadly rounded; chambers few, 5 to 6 in last formed whorl, increasing rapidly in size as added, last formed one constituting approximately a third of the test, last 1 or 2 somewhat inflated; sutures rather indistinct between early chambers, distinct and slightly depressed between later ones; surface somewhat hyaline, very finely and closely perforate, with a distinct lunate area on the last formed chamber above the aperture; aperture a large rather wide elliptical opening at the base of the last formed chamber in the ventral umbilicate region, a number of distinct dentitions on the margin of the early chambers at the base of the aperture, occasionally extending beyond the apertural area and ornamenting the entire test.

Average length, 0.80 mm.; breadth, 0.57 mm.; thickness, 0.55 mm.

Remarks.—This is one of several common species in the fauna. It seems quite close to *Baggina californica* Cushman, known from the middle and upper Miocene of California. However, it differs in that there are distinct dentitions at the base of the aperture which occasionally extend out onto the surface of the test. This feature is somewhat developed on *Baggina totomiensis* Makiyama from the lower Pliocene of Japan. However, this species differs from the present one in that the aperture is narrower and the final chamber considerably larger.

Although these three species seem quite closely related, they are nevertheless distinct. Possibly these distinctions are evolutionary trends which reflect environmental differences.

Occurrence.—Astoria formation in a new road cut adjacent to state highway 9, some 2 miles northeast of the junction of U. S. highway 101 and state highway 9, Grays Harbor County, Washington.

Syntypes.—State University Iowa, 6785 and 6786 (both figured specimens).

Family CASSIDULINIDAE
Genus PULVINULINELLA Cushman, 1926
PULVINULINELLA PARVA
Cushman and Laiming
Plate 119, figures 12–14

Pulvinulinella parva CUSHMAN and LAIMING, 1931, Jour. Paleontology, vol. 5, p. 115, pl. 13, figs. 5a–c; KLEINPELL, 1938, Miocene Stratigraphy of California, *published by* Am. Assoc. Petroleum Geologists, p. 329.

Pulvinulinella cf. *smithi* R. E. and K. C. STEWART, CUSHMAN and PARKER, 1931, Cushman Lab. Foram. Research Contr., vol. 7, pt. 1, p. 14, pl. 2, figs. 12a–c.

Dimensions.—Diameter, 0.35 mm.; thickness, 0.13 mm.

Remarks.—Although somewhat rare, a few quite well preserved specimens possess all the characteristics of *Pulvinulinella parva* Cushman and Laiming. Typically they have a more or less flattened dorsal side which is distinctly raised in the umbonal region. Also, the ventral side is strongly convex; there is a distinct keel; the sutures are more distinct ventrally than dorsally; and the aperture is a slit-like opening very near the keel and in the plane of coiling.

As one of the California species in the fauna, it seems quite significant. *Pulvinulinella*, being a temperate-to-cold-water genus, would very likely be found in the Astoria of Washington. This particular species probably represents a relatively warm water form which existed somewhat successfully at least as far north as southern Washington during the Miocene.

Occurrence.—Astoria formation in a new road cut adjacent to state highway 9, some 2 miles northeast of the junction of U. S. highway 101 and state highway 9, Grays Harbor County, Washington. Known previously from the lower Miocene of California, the Astoria formation in Oregon, and the type Blakely formation of Washington (see Kleinpell, 1938, p. 329, for specific localities).

Figured specimen.—State Univ. Iowa, 6787.

Genus CASSIDULINA d'Orbigny, 1826
CASSIDULINA PULCHELLA d'Orbigny
Plate 119, figures 21–23

Cassidulina pulchella d'Orbigny, CUSHMAN, 1925; Cushman Lab. Foram. Research Contr., vol. 1, pt. 2, p. 34, pl. 5, fig. 16.

Cassidulina cf. *pulchella* d'Orbigny, KLEINPELL, 1938, Miocene Stratigraphy of California, published by Am. Assoc. Petroleum Geologists, p. 336, pl. 17, figs. 14, 15.

Description.—Test nearly circular in side view, equally biconvex in cross section, periphery very slightly keeled; chambers fairly distinct, 6 to 7 pairs in last formed whorl, somewhat kidney-shaped, only slightly if at all inflated; sutures narrow, nonlimbate, rather distinct between last few chambers, indistinct between earlier ones, curved considerably, especially near umbo; surface hyaline, very finely perforate, with translucent umbo most pronounced on ventral side; aperture a distinct rather broad slit-like opening parallel to the plane of coiling.

Average diameter, 0.60 mm.; thickness, 0.32 mm.

Remarks.—This species is by far the most common one in the fauna. It is equally abundant in all samples.

There are, throughout the literature, a number of widely varied specimens figured as *Cassidulina pulchella* d'Orbigny. It is therefore apparent that this name has grown to include a large group of *Cassidulina* varying greatly in form. A specimen from the Monterey shale of California (Cushman, 1925, p. 34, pl. 5, fig. 16) and one previously compared with this species from the middle Miocene of California (Kleinpell, 1938, p. 336, pl. 17, figs. 14, 15), are the only two which are essentially identical with those from the Astoria of Washington. It perhaps would be best to refer these Miocene specimens to a new species, but inasmuch as California material is not at hand for study, the present specimens are being referred to as the middle Miocene form of *C. pulchella*.

Occurrence.—Astoria formation in a new

road cut adjacent to state highway 9, some 2 miles northeast of the junction of U. S. highway 101 and state highway 9, Grays Harbor County, Washington, and known previously from the middle Miocene of California. Other specimens referred to this species are from the lower and upper Miocene of California, the Pliocene of California, and Recent deposits off the Pacific Coast. The type is from Recent deposits off the Coast of Peru.

Figured specimen.—State Univ. Iowa, 6788.

Family ANOMALINIDAE
Genus CIBICIDES Montfort, 1808
CIBICIDES aff. C. PERLUCIDA Nuttall
Plate 119, figures 18–20

? *Cibicides perlucida* NUTTALL, 1932, Jour. Paleontology, vol. 6, p. 33, pl. 8, figs. 10–12.
? *Cibicides* aff. *C. perlucida* Nuttall, KLEINPELL, 1938, Miocene Stratigraphy of California, published by Am. Assoc. Petroleum Geologists, p. 355.

Description.—Test rotaliform, biconvex, dorsal side somewhat raised in central region but nearly flat on last formed whorl, ventral side strongly convex, periphery subacute; chambers distinct ventrally and last formed whorl dorsally, 10 to 11 in last formed whorl, increasing gradually in size as added, last 1 or 2 very slightly inflated; sutures somewhat limbate, distinct ventrally and between chambers of last formed whole whorl dorsally, slightly curved, approaching periphery on dorsal side more or less obliquely; surface rather coarsely perforate, umbo of translucent material; aperture a small low slit-like slightly arched opening extending from the periphery a short distance toward the umbilicus.

Diameter, 0.50 mm.; thickness, 0.25 mm.

Remarks.—Several incomplete specimens of *Cibicides* are perhaps most similar to *C. perlucida* Nuttall. The general shape of the test, character of the sutures, and arrangement of chambers are somewhat similar to Nuttall's species. However, the Astoria specimens are only about half the size given as the average for *C. perlucida;* the aperture extends only a short distance toward the umbilicus; and only the chambers of the last formed whorl are distinct on the dorsal side. The size variation is perhaps the major distinction between the two forms.

Cibicides altamiraensis Kleinpell, from the Altamira shale of California (Kleinpell, 1938, p. 351, pl. 19, figs. 4, 5, 8) superficially resembles this Astoria form. Nevertheless, a detailed comparison reveals considerable distinction between the two. The present specimens are distinctly raised in the umbonal region of the dorsal surface; the foraminae are all the same size; the sutures are flush with the surface and do not curve forward near the periphery on the dorsal side. All of these features are absent on *C. altamiraensis.*

Since the form under consideration is represented by a few, rather poorly preserved specimens, a definite classification is not possible at this time. Nevertheless, the similarity expressed between the present form and *C. perlucida,* suggests a close relationship. *C. perlucida* may be ancestral to the Astoria form.

Occurrence.—Astoria formation in a new road cut adjacent to state highway 9, some 2 miles northeast of the junction of U. S. highway 101 and state highway 9, Grays Harbor County, Washington. The type *C. perlucida* came from the Alazan shale of the Tampico Embayment, Mexico. Kleinpell has recorded a form from the lower Miocene of California as having affinities with *C. perlucida.*

Figured specimen.—State Univ. Iowa, 6789.

REFERENCES

BECK, R. S., 1943, Eocene Foraminifera from the Cowlitz River, Lewis County, Washington: Jour. Paleontology, vol. 17, pp. 584–614, pls. 98–109, 4 text figs.

CUSHMAN, J. A., 1925, Some Textulariidae from the Miocene of California: Cushman Lab. Foram. Research Contr., vol. 1, pt. 2, pp. 29–34, pl. 5.

——, 1940, Foraminifera, their classification and economic use; 3rd ed.: Harvard Univ. Press, pp. 1–535, pls. 1–48.

——, and LAIMING, B., 1931, Miocene Foraminifera from Los Sauces Creek, Ventura County, California: Jour. Paleontology, vol. 5, pp. 79–120, pls. 9–14, 5 text figs.

——, and PARKER, F. L., 1931, Miocene Foraminifera from the Temblor of the east side of the San Joaquin valley, California: Cushman Lab. Foram. Research Contr., vol. 7, pt. 1, pp. 1–16, pls. 1–3.

ELLIS, B. F. and MESSINA, A. R., 1940 Catalogue of Foraminifera: Spec. Publ. Amer. Mus. Nat. History, vols. 1–30.

ETHERINGTON, T. J., 1931, Stratigraphy and

fauna of the Astoria Miocene of southwest Washington: California Univ., Dept. Geol. Sci. Bull., vol. 20, pp. 31–114, 14 pls.

GALLOWAY, J. J., 1933, A manual of Foraminifera: James Furman Kemp Memorial Ser. Publ. no. 1, Principia Press, Univ. Ind., pp. 1–483, pls. 1–42.

——, and MORREY, M., 1929, A Lower Tertiary Foraminiferal fauna from Manta, Ecuador: Bull. Am. Paleontology, vol. 15, no. 55, pp. 7–56, pls. 1–6.

KLEINPELL, R. M., 1938, Miocene stratigraphy of California: Am. Assoc. Petroleum Geologists, pp. 1–450, 22 pls.

RAU, W. W., 1948, Foraminifera from the Porter shale (Lincoln formation), Grays Harbor County, Washington: Jour. Paleontology, vol. 22, pp. 152–174, pls. 27–31, 1 text fig.

WEAVER, C. E., 1937, Tertiary stratigraphy of western Washington and northern Oregon: Washington Univ. (Seattle) Publ. in Geol., vol. 4, pp. 1–266.

WEAVER, C. E., and others, 1944, Correlation of marine Cenozoic formations of western North America: Geol. Soc. America Bull., vol. 55 pp. 569–598, 1 pl.

JOURNAL OF PALEONTOLOGY, VOL. 22, NO. 6, PP. 783–791, PLS. 120, 121, NOVEMBER 1948

MOLLUSCAN FAUNULE FROM DEVONIAN ISLAND MESA BEDS, ARIZONA

ALEXANDER STOYANOW
University of Arizona

ABSTRACT—The Island Mesa beds contain a rather fragmentary but singular Late Devonian faunule of lamellibranchs and gastropods. The following four new genera and their genotypes, representative of the faunule, are described: 1. *Congeriomorpha andrusovi*, a mytiloid lamellibranch with an acute carina and an anterior lobe, both terminal, but also provided with a subumbonal myophoric depression as in the Dreissensiidae (not the "septum" *auctorum*, however, since a true umbonal cavity is not developed below the myophoric depression notwithstanding its considerable elevation above the valve interior), to which was attached not only the anterior adductor, as in the typical species of the latter family, but also, separated by a vertical ridge, the anterior retractor; dentition in the genotype represented only by weak posterior laterals; 2. *Tusayana cibola*, a lamellibranch of unestablished relationship with a circular outline, a broad hinge plate carrying strong amorphous cardinals behind an oval anterior adductor scar, strong posterior laterals, and a narrow opisthodetic ligament; 3. *Arizonella allecta*, a pleurotomariid gastropod essentially differing from *Büchelia* Schlüter in having an unchanneled inner lip, an outer lip with an acute V-shaped sinus placed on a carina above the peripheral angle instead of a true selenizone on the periphery with a groove above, and in the presence of a revolving salient midway between the upper suture and the periphery; 4. *Arastra torquata*, a trochiform gastropod which is distinguished from the species referable to *Orecopia* Knight by a reversed outline of the outer lip with a forward convexity above the periphery and a true selenizone on the peripheral angle, and also by the development of overlapping frills at the peripheral angle in the advanced stages.

INTRODUCTION

THE original definition of the Island Mesa beds (Stoyanow, 1936, p. 500; Wilmarth, 1938, p. 1028) is presented below with a few changes.

Using the Jerome formation as the standard for the Devonian of north-central Arizona, and proceeding from Jerome northeastward, the observer finds that: (1) the thickness of Devonian strata decreases toward the San Francisco Mountains and Flagstaff, and (2) the limestone beds persistently become impure and more arenaceous in that direction. Already twelve miles northeast of Jerome, on the Verde River and southwest of Island Mesa, the increase of arenaceous matter in the upper part of the Devonian is appreciable. The little shells of *Camarotoechia eximia* and *C. saxatilis* found in limestone at Jerome invariably occur in sandstone here. Even more striking is the faunal aspect of the uppermost layers. The usual complex of the Upper Devonian fauna of the Jerome formation is at hand, but within 125 feet below the base of the Mississippian Redwall limestone are 40 feet of grayish-lavender, thin-bedded, shaly limestone and shale, overlain by 8 feet of massive, arenaceous, purplish-gray limestone which contains a rich and exceptional fauna of lamellibranchs and gastropods. That this new faunule is still within the Devonian is evidenced by the presence of such forms characteristic for the Late Devonian as *Aglaoglypta maera* (Conrad), Pl. 2, fig. 30. Above these beds are: purplish arenaceous shale about 11 feet in thickness, and ledge-forming arenaceous limestone and sandstone of the same color, 64 feet thick. This terminal part of the Devonian of north-central Arizona, resting beneath the base of the Redwall in the abrupt cliff of the Colorado Plateau and attaining a thickness of about 122 feet, has not been located at Jerome. It is characterized by a peculiar assemblage of Mollusca and is designated as the Island Mesa beds of the Jerome formation.

The purpose of the present paper is to record all that can be inferred from the incomplete Island Mesa specimens thus far obtained. No attempt is made at this time to place the four species described below, and apparently belonging to new genera, within the established supergeneric systematic groups.

It is a pleasure to express my thanks to Dr. J. Brookes Knight and Dr. N. D. Newell with whom I corresponded during my studies.

PALEONTOLOGICAL DESCRIPTION

CONGERIOMORPHA Stoyanow, n. gen.
Genotype, *Congeriomorpha andrusovi* Stoyanow, n. sp.

In general appearance the shells of this genus resemble certain representatives of the family Dreissensiidae Gray. They are much like *Congeria balatonica* (Partsch) as illustrated by Andrusov (1897, p. 129, Pl. 4, figs. 19–25) in that they are subrhombic-oval in outline and carinate.[1] They differ, however, in the presence of anterior lobes which are as strongly developed as in *Volsella*. Both the anterior lobes and the acute visceral carina[2] are terminal. In this relation *Congeriomorpha* has characteristics of both, *Volsella* and *Mytilus* (Pl. 120, fig. 2).

On the anterior surface of the umbonal region there is a wrinkled "cordiform" depression which, in the apical half of each valve, is outlined by a faint furrow limiting the anterior lobe on its inner side and subconcentric to the main carina, but posteriorly grading into a strong, coarse, and elevated ridge which, as it extends to the anterior margin, markedly diverges from the course of the carina (Pl. 120, fig. 1). This outline of the anterior depression corresponds with Andrusov's (1897, p. 221, Pl. 12, fig. 13) "lunuleform curve" of certain Dreissensiidae and the depression itself with his "pseudolunula" (*ibidem*, p. 40).[3] Since this anterior depression in its outline is unlike a lunule, and in its size and relative position to the other parts of the shell resembles more the escutcheon in the posterior part of *Trigonia*, the term "scute" is applied to it in this paper.

The most outstanding characteristic of this genus is the subumbonal myophoric depression. Andrusov (1897, p. 41) called the subumbonal depression in Dreissensiidae a septum because *in most* of the species of that family there is an actual and well developed umbonal cavity under it. Woods

[1] According to Andrusov (*ibidem*, p. 204) his groups "Rhomboideae" and "Subglobosae" are not distinctly separable.

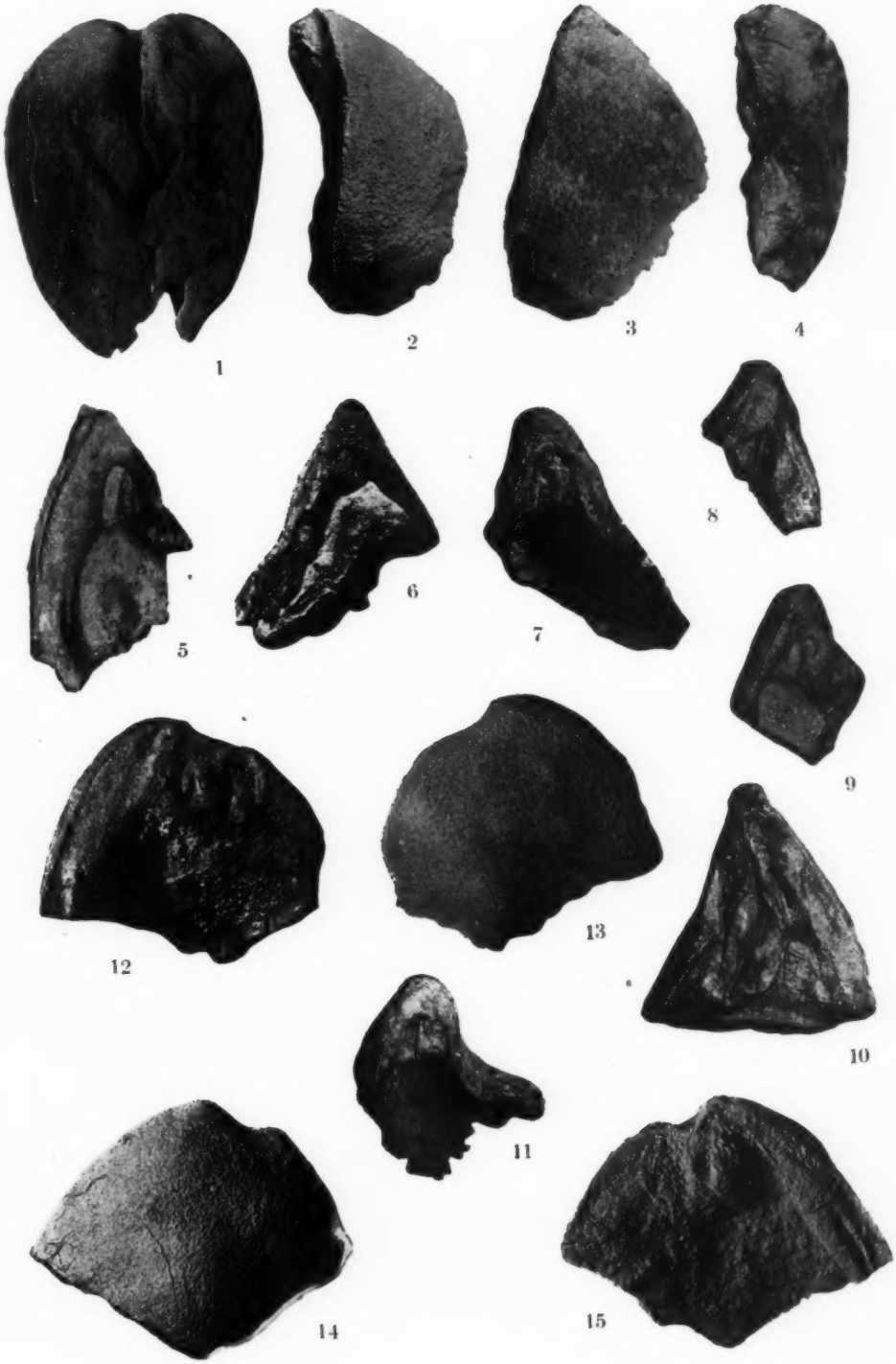
[2] I do not use here "umbonal ridge," a term proposed by Newell (1942, p. 25) for the ridge in mytiloid shells which is essentially developed in their umbonal part. In *Congeriomorpha*, as in many species of the *Dreissensiidae*, the carinae are acute and almost equally strong from the respective beaks to the ventral margin.

[3] In more recent literature a similar depression in *Congeria subglobosa* (Partsch) is referred to as a lunule (Davies, 1935, p. 190, fig. 261 f.).

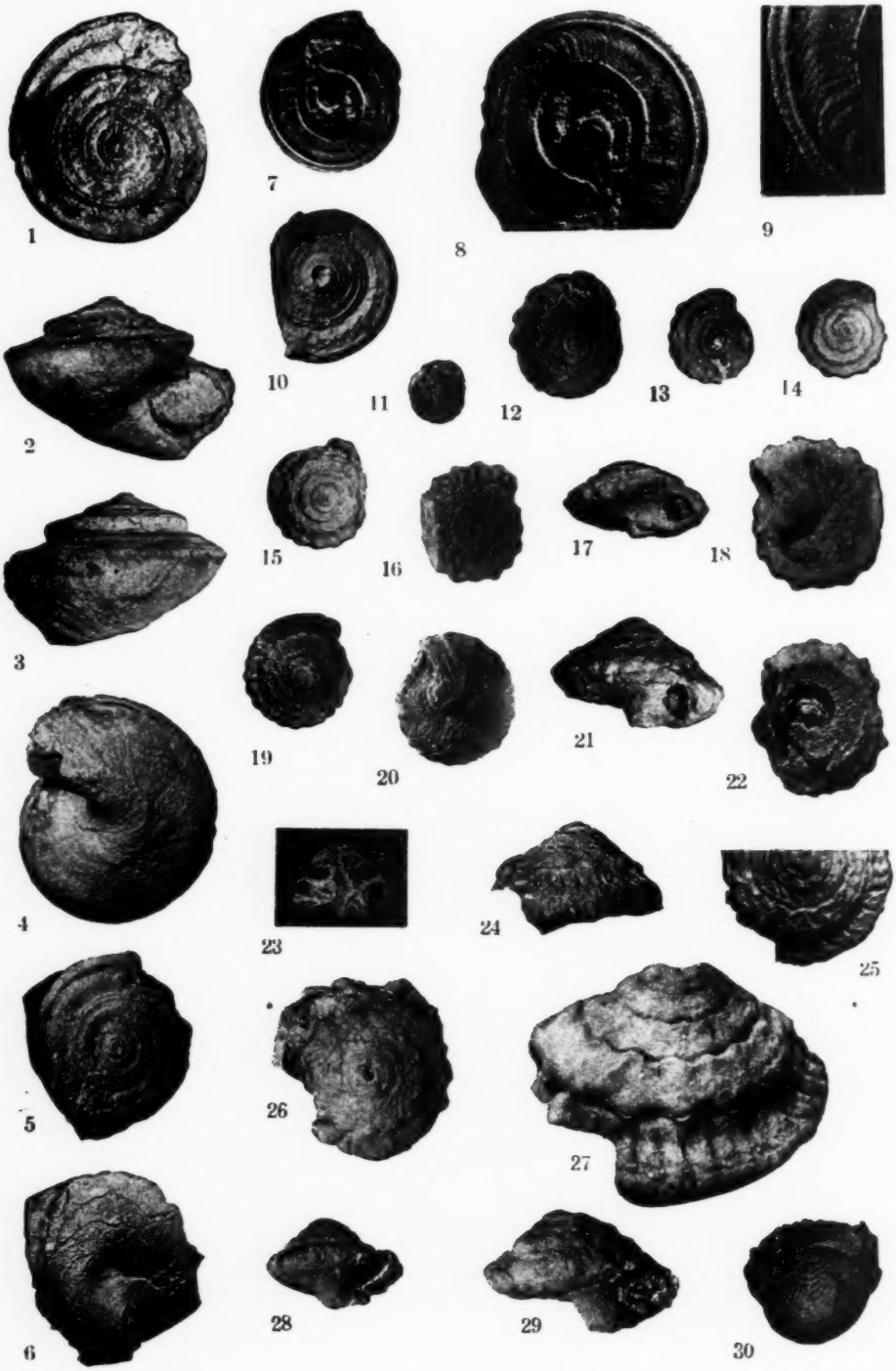
EXPLANATION OF PLATE 120

FIGS. *1–11*—*Congeriomorpha andrusovi* Stoyanow, n. sp., syntypes. *1–4*, No. IMB.1. *1*, Anterior view of both valves, ×1.1. Note the cordiform outline of the scute, faint in the umbonal region but ridge-like ventrally, and the coarse wrinkles passing from the scute across a depression to the carina. *2*, The left valve. To show a strong depression between the acute carina and the anterodorsal lobe, and the growth lines in the ventral region. *3*, The visceral surface of the left valve. *4*, Side view of the left valve showing the depressed scute and the byssal notch. *5*, No. IMB.2, left valve. Note the myophoric depression separated by a vertical ridge into an elevated anterior part for the anterior adductor and a sunken posterior part for the retractor, a narrow ligamental groove, and a weak posterolateral tooth. *6*, No. IMB.3, right valve, ×1.1, showing the myophoric depression. *7*, No. IMB.4, left valve, ×1.1, to show a deeply sunken posterior part of the myophoric depression for the retractor. *8*, No. IMB.5, left valve showing a strongly developed vertical ridge on the myophoric depression. *9*, No. IMB.6, left valve with an asymmetrically divided myophore. *10*, No. IMB.7, right valve. Note the "path" of three consecutive myophoric depressions with inadequately developed and missing vertical ridges, and three successive outlines of the scute. *11*, No. IMB.8, left valve. To show a nearly symmetrically divided myophoric depression. (p. 786)

12–15—*Tusayana cibola* Stoyanow, n. sp., the holotype, No. IMB.9. *12*, interior of the left valve. Note the hinge plate with the oval anterior adductor scar, the bifid cardinal tooth, the deltoid tooth, the posterior socket, the narrow ligamental groove, the excentric posterolateral tooth, and the posterolateral socket with an incipient lamina. *13*, exterior of the left valve. *14*, exterior of the right valve. *15*, interior of the right valve. Note the strong posterolateral tooth limited by sockets and passing upward into a ridge which fits in the posterior socket on the hinge plate of the left valve, the trigonal socket for the reception of the deltoid tooth of the left valve, the compound cardinal tooth, the lunule, and the bordered oval scar of the anterior adductor. (p. 788)



Stoyanow, Devonian Mollusca



Stoyanow, Devonian Mollusca

(1903, pp. 111–112) used terms "umbonal septum" and umbonal plate" for the myophoric depression in *Dreissensia lanceolata* (Sowerby). Davies (1935, p. 191) applied to it the name "myophoric septum" for *Congeria*, whereas Stephenson (1941, p. 157) described a similar structure in *Cuneolus* Stephenson as "septal depression," and Newell (1942, p. 25 and p. 76) discussed as "umbonal septum" and "umbonal deck" the homoeomorphic structures in certain Paleozoic Mytilacea. None of these terms is applicable to the homologous structure in *Congeriomorpha* for the simple reason that in this genus the space corresponding to the umbonal cavity is completely filled with shelly matter and, therefore, there is no umbonal cavity, and consequently, no septum or plate. However, not all species of Dreissensiidae possess a deep umbonal cavity. Andrusov has pointed out its absence in *Congeria nucleolus* Rzehak, *Dreissensia eichwaldi* Issel, and *D. retowskii* Andrusov (*see* Andrusov, 1897, p. 45; p. 188, Pl. figs. 25–28; p. 320, Pl. 7, figs. 22–24 and Pl., 17, figs. 21–24; p. 316, Pl. 17, figs. 18–20).

The myophoric depression of *Congeriomorpha* is sharply separated into anterior and posterior parts by a vertical ridge in such a way that the floor of the anterior

---

EXPLANATION OF PLATE 121

FIGS. *1–10*—*Arizonella allecta* Stoyanow, n. sp., syntypes. *1–4*, No. IMB.13, *1*, apical view. Note the revolving salient midway between the upper suture and the peripheral angle, the carina, the pseudo-selenizone, and the increase in sutural dip in the last whorl. *2*, apertural view showing the unchanneled columellar lip. *3*, side view to show growth lines below the periphery of the last whorl and the steep wall of the penultimate whorl. *4*, umbilical view. Note the semilunar ridge, a nearly complete filling of the umbilical depression with the columellar inductura, the fissural contact between the latter and the semilunar ridge, and the course of growth lines. *5*, *6*, No. IMB.14, *5*, apical view. The revolving salient limited on both sides by depressions, the acute carina, and the narrow pseudo-selenizone are observable in nearly all whorls. *6*, umbilical view showing a phaneromphalous umbilicus between the semilunar ridge and the columellar inductura. *7–9*, No. IMB.15. *7*, apical view showing the revolving salient, the carina, the pseudo-selenizone, and the upper margin of the outer lip delineated by the growth lines. *8*, the same enlarged, ×1.5, to show the margin of the outer lip above the peripheral angle. *9*, enlargement of a part of the same, ×2.7, showing details of the outer lip. Note the sickle-shaped backward obliquity between the upper suture and the carina, the acute V-shaped sinus on the carina, and the straight course of the outer lip on the pseudo-selenizone without the formation of lunulae. *10*, No. IMB.16. Apical view. Note the growth lines on the last observable whorl. (p. 790)

11–29—*Arastra torquata* Stoyanow, n. sp., syntypes. *11–12*, No. IMB.17. *11*, apical view. *12*, enlargement of the same, ×2, to show the growth lines abutting against the selenizone and the gradual development of peripheral frills in the last observable whorl. *13–15*, Nos. IMB.*18–20*, apical views showing variations in the development of the frills with the growth. *16–18*, No. IMB.21. *16*, apical view, ×1.2. Note the increment of shelly matter on the lines of growth with a backward obliquity, and the frills. *17*, apertural view, ×1.4, showing the columellar lip and the sinus at the periphery. *18*, umbilical view, ×1.6, to show the phaneromphalous umbilicus between the columella and the semilunar ridge. *19–21*, No. IMB.22. *19*, apical view showing the frills and the selenizone (in the later part of the last whorl). *20*, umbilical view, ×1.2. Note the course of the growth lines below the periphery. *21*, apertural view, ×1.5, showing the columellar lip. *22*, No. IMB.23, apical view ×1.5, with the spire removed to show the acute upper margin of the whorl. Note the trapezoidal section of the latter. *23*, No. IMB.24. A columellar section, ×1.3, to show the trapezoidal whorl sections and the tortuous umbilicus. *24*, *25*, No. IMB.25. *24*, side view. Note the shallow lunulae formed by the outer lip on the selenizone at the peripheral angle as delineated by the growth lines. *25*, apical view showing the sickle-shaped backward obliquity of the outer lip above the peripheral angle and the upper border of the selenizone. *26*, No. IMB.26. Apical view, ×1.5, showing the frills and the upper border of the selenizone. *27*, the same as figs. *24–25*, side view, ×2, to show the lappets on the frills of the penultimate whorl, the forward convexity of the outer lip above the periphery (in the right part of the last whorl), the selenizone bordered above (dark vertical lines are fissures filled with black material), and the depression in the whorl between the upper suture and the selenizone. *28* and *29*, No. IMB.27, ×1.8, and No. IMB.28, ×1.5. Apertural views to show the columellar lip and the parietal inductura. (p. 790)

30—*Aglaoglypta maera* (Conrad). A plesiotype collected with the faunule of the Island Mesa beds. Apertural view, ×1.3. (p. 783)

part is on a level with the top of the ridge, whereas the posterior part is appreciably depressed, the ridge itself forming a vertical flexure between the two parts (Pl. 120, figs. 5–9 and 11). It may be presumed that the anterior, more elevated part served for the attachment of the anterior adductor muscle, whereas the anterior retractor was attached to the posterior and sunken part. Generally, in *Congeria* the latter muscle is attached to the apophysis which itself is a terminal and exposed part of the sub-septal keel usually invisible from above. In *Dreissensia* the same muscle is attached, with a few exceptions, to the under surface of the septum.

Against the above interpretation of the myophoric depression in *Congeriomorpha* is the fact that in the two mentioned genera of Dreissensiidae there are also species known which have both a well developed apophysis and also a divided septum. The latter condition is more strongly developed in certain species of *Congeria* and much less so in *Dreissensia*. Species of *Congeria* with a vertically divided septum include: *Congeria turgida* Brusina, *in* Andrusov (1897, p. 42, p. 111, Pl. 3, fig. 4); *C. balatonica* (Partsch), *ibidem* (p. 129, Pl. 4, fig. 20, structure not mentioned in the text but identifiable in the illustration); and *C. subglobosa* (Partsch), *ibidem* (p. 42, p. 220, Pl. 12, figs. 12–16, structure mentioned in the text but not visible in the illustration). On the other hand species like *Congeria* (*?*) *scrobiculata* Brusina, one of the "isolated forms" of Andrusov (*ibidem*, p. 231, Pl. 16, figs. 27–30), have the anterior retractor attached to the septum and not to the apophysis.

The functional myophoric depression may occur either close to the beak or at an appreciable distance from it. One of my illustrations of *Congeriomorpha andrusovi*, n. sp. Pl. 120, fig. 10, shows the "path" of successive myophoric depressions. When the earlier depressions are covered with shelly matter there is a more or less smooth space between the beak and the functional myophoric depression. A similar development apparently is present in the shell of *Congeria ungula caprae* (Goldfuss and Münster) as illustrated by Andrusov (1897, p. 158, Pl. 5, figs. 18 and 20).

On the main interior surface of some of the described specimens a very faint scar or depression is situated below the posterior part of the dorsal margin which corresponds in position with the "upper" (dorsal) lobe of the posterior adductor in some *Mytilacea*.

The ligamental groove is very narrow and concentric with the dorsal margin (Pl. 120, fig. 5). Unlike the Cretaceous *Cuneolus* Stephenson (1941, p. 157, Pl. 25, figs. 22 and 23), originally decribed by Conrad as a species of *Dreissensia* or *Dreissena*, the ligamental groove of *Congeriomorpha* does not continue under the beak and across to the anterior margin, but dies out before reaching the anterior lobe.

One posterolateral tooth separates two sockets on the relatively wide hinge plate of the right valve, and correspondingly, a socket bordered by two weak laminae occurs in the left valve.

In common with the *Dreissensiidae*, *Congeriomorpha* has a myophoric depression. It differs essentially from the genera of that family by:

1. Presence of an anterior lobe.
2. Absence of the umbonal cavity under the myophoric depression.
3. Presence of posterolateral teeth.

Congeriomorpha appears to differ from the *Mytilidae* in having a myophore (which apparently was functional and not merely a connecting brace), a scute, and posterolateral teeth.

CONGERIOMORPHA ANDRUSOVI
Stoyanow, n. sp.
Plate 120, figures 1–11

In the Island Mesa beds all fossils are thoroughly silicified and the original shell structure is not preserved in any of the collected specimens. The shells of *Congeriomorpha andrusovi* are very brittle, especially their comparatively thinner ventral parts. They are almost invariably fractured and recemented. The recemented parts are held together by their calcareous internal molds and usually leaching in dilute hydrochloric acid, undertaken to expose the internal characters, causes the ventral parts of the valves to fall to pieces.

Of the eight illustrated specimens the syntype No. IMB.1 (Pl. 120, figs. 1–4) consists of both valves which were collected together in the matrix but not in juxtaposition and in which the exterior is better pre-

served. In other syntypes the thin ventral part of the valves was destroyed during the leaching, but they show well the principal characteristics of the interior in the umbonal region and their variations. The syntypes shown on Plate 120 by figures 5, 7, 8, 9, and 11 are left valves, whereas figures 6 and 10 of the same plates illustrate the interior of right valves.

Shells of this species are of medium size, the greatest dimension observed is 60 mm. from the beak to the somewhat eroded ventral margin. The left valve probably is less inflated than the right, at least it appears to measure less across the anterior surface in the syntype No. IMB. 1. Beaks are terminal and usually are separated from the anterior lobe by a depression, but sometimes their acuteness is impaired by a stronger development of the anterior lobe. In such forms the umbo has a somewhat blunt appearance. The dorsal margin of the shell is very slightly curved, sometimes almost straight, and passes into the posterior margin by a gentle convex curve. The ventral margin is semioval, and the anterior margin is concave. The surface of the valves slopes gradually toward the dorsal and posterior margins but descends abruptly from the carinae to the anterior thus forming the anterior face of the carinae shell with appreciable depressions between the carinae and the scute.

The main outer surface of the valves is smooth except for faint lines of growth in the ventral region (Pl. 120, fig. 2). The anterior surface is also smooth in the umbonal part, but the scute and the antero-ventral surface are strongly wrinkled (Pl. 120, figs. 1 and 4). As stated in the description of the genus, in the umbonal part of the anterior surface the scute is outlined only by faint grooves which are concentric with the carinae and which separate the scute from the anterior lobes. Ventrally, however, these grooves pass very rapidly into strong ridges which turn away from the carinae toward the anterior margin, in this way producing a cordiform outline of the scute, as in *Congeria* (Andrusov, 1897, Pl. 4, fig. 22, Pl. 12, fig. 13; Zittel, 1927, p. 464, fig. 734; Davies, 1935, p. 190, fig. 261f) which is quite different from the oval scute of the falcate *Dreissensia*-like shells (Woods, 1903, vol. 1, Pl. 19, fig. 1b; Stephenson, 1941, Pl. 25, fig. 24). These ridges are crossed by coarse wrinkles that pass from the scute across the anteroventral surface to the carinae beyond which they merge into ordinary growth lines on the main surface and die out. Sometimes there are two or even three concentric ridges within the latest outline of the scute (Pl. 120, figs 4 and 10). The position of the rather irregular byssal gape is low on the scute.

The individual growth development was quite irregular and is especially pronounced in the variable strength of the growth lines and wrinkles on the scute which is also variable in depth. Internally variations are observable in the elevation of the anterior half of the myophoric depression above its posterior half. In a few of the studied specimens, especially in those that show indications of rapid growth (Pl. 120, fig. 10), the dividing vertical ridge is not adequately developed and it is irregular, or even altogether missing.

I am not aware of any Paleozoic lamellibranchs that can be readily compared with this species.

TYPE.—Syntypes: Nos. IMB.1–IMB.8.

TUSAYANA Stoyanow, n. gen.
Genotype, *Tusayana cibola* Stoyanow, n. sp.

This genus and species are based on both valves of the holotype and three paratypes represented only by right valves.

The shell is almost equilateral, of medium size and moderate thickness. Although the ventral part of the valves is not preserved in any of the specimens, the nearly equal inclination of the shell in all directions from the most elevated central area indicates a subcircular outline. The surface of the shell is smooth, the umbones are moderate, the prosogyral, small, pointed beaks are located centrally and above a small but well excavated lunule, the opisthodetic and narrow ligamental groove is exposed and concentric with the posterodorsal margin, and the valves are thick in the umbonal region but become thinner in the posteroventral direction; such features occur in many lamellibranchs of distant relationships, the characteristics of the interior are more important.

On the strongly developed hinge plate of the left valve there is the deep oval scar of

the anterior adductor muscle posterior to which are two cardinal teeth, one bifid and the other long and simple. The relatively large compound cardinal tooth of the right valve is amorphous. Posterolateral teeth are present in both valves. There is no cavity under the hinge plate. The position of the posterior adductor scar could not be determined with certainty.

The character and relative position of the anterior adductor scar, teeth, and lunule, discussed in more detail in the description of the genotype, are not unique in Paleozoic genera. They are to a certain extent suggestive of similar structures in some Late Paleozoic *Cypricardiacea*, and in other genera with transitional and less definitely established characteristics which are referred to *Cyrtodontidae* or even *Modiolopsidae*. Thus, a similar development of a strong hinge plate with a bifid cardinal tooth situated between an oval anterior adductor scar and a narrow subtrigonal cardinal tooth occurs in the left valve of *Ischyrodonta decipiens* Ulrich (1893, p. 673, Pl. 54, fig. 19). This species, without posterolateral teeth but with a cavity under the hinge plate, was compared by Ulrich to "*Ortonella*" *hainesi* (Miller), a form with a lunule, posterolateral teeth, a narrow hinge plate, and an anterior adductor scar placed apparently in the main depression of the valves (*ibidem*, p. 670, Pl. 53, fig. 11), whereas the hinge of *Modiolodon oviformis* Ulrich (1893, p. 652, Pl. 53, figs. 7 and 8; 1897, p. 521, fig. 40g), with a more sunken anterior adductor scar probably off the hinge plate, was also compared with that in *Ischyrodonta*. However, these and similar pre-Devonian forms with even less individualized hinge plates, invariably have elongate and very inequilateral shells with deeper placed ligamental grooves; whereas those with a less elongate or even subcircular outline have even more reduced hinge plates and the muscle scars not on the hinge plate but on the main floor of the valves. Among Late Paleozoic *Cypricardiacea* are certain genera in which the general arrangement of dentition corresponds fairly to those under consideration. In the genotype of *Pleurophorus* King (1850, p. 180, Pl. 15, figs. 16–17) the oval and deep anterior adductor scar is outlined by a ridge, and the interrelation of the cardinal teeth and their sockets is quite similar, the posterolateral teeth also are distinct from the exposed ligamental groove, and there is a lunule under the beaks, but the shape of the shell and other diagnostic characteristics do not permit a closer comparison.

TUSAYANA CIBOLA Stoyanow, n. sp.
Plate 120, figures 12–15

The two valves of the holotype were collected close together but not in juxtaposition and may belong to different individuals. However, the right and left counterparts agree precisely.

Left valve.—What first attracts attention in the left valve is the development of a strong hinge plate (Pl. 120, fig. 12). It is very broad in the umbonal part and also quite wide in the posterodorsal part. The concave and deepest portion of the main interior of the valve is excentric and is situated directly below the angle of meeting of these two parts. From there the floor of the depression gradually rises toward the anterior margin of the shell until it attains the level of the hinge plate. This relationship makes the hinge plate especially prominent and elevated in the umbonal and posterior parts of the valve.

Starting from the anterior margin the following features are distinguished in the hinge plate: 1. Oval and deeply impressed scar of the anterior adductor muscle; 2. On the elevated platform behind the scar and below the lunule is a general shallow oval depression in which occurs a bifid cardinal tooth the anterior branch of which is much more prominent and elevated; 3. Behind the depression and directly in line with the beak is an elevated trigonal or "deltoid" tooth; 4. Posterior to the deltoid tooth is a shallow, long, and narrow depression or socket which is more or less concentric with the posterodorsal margin of the valve; 5. Behind this depression the posterior part of the hinge plate is nearly flat in its umbonal part but ventrally, considerably distant from the ligamental groove, it develops a strong and somewhat excentric posterolateral tooth and a socket within which is a weak or incipient lamina or ridge.

Right valve.—In the right valve the hinge plate is much less individualized except in the posterodorsal region. The scar of the

anterior adductor muscle is of the same size and outline as in the left valve. It is limited anteriorly by a fine narrow and slightly elevated border, and posteriorly by the buttress of the compound cardinal tooth. The latter is large, amorphous, and bifid. Its anterior part is a lower and crescentic ridge which, in the central part of the tooth, is separated by a deep pit from the stronger and considerably more elevated posterior part. This tooth opposes the oval depression (2) in the hinge plate of the left valve in such a way that the anterior branch of the bifid cardinal tooth of the latter valve fits in the central pit of the amorphous tooth. Posterior to the latter tooth is a more or less trigonal socket for the reception of the deltoid tooth of the left valve (3). Between this socket and the ligamental groove, on the posterior part of the hinge plate, is a weak and low ridge which is concentric with the posterodorsal margin and fits in the long depression (4) of the left valve. Posteroventrally this ridge grades into a strong posterolateral tooth which is limited on both sides by sockets.

Type.—Holotype: No. IMB.9 (left and right valves); Paratypes (not illustrated, right valve only): Nos. IMB.10–IMB.12.

ARIZONELLA Stoyanow, n. gen.
Genotype, *Arizonella allecta* Stoyanow, n. sp.

The gastropod shells for which this genus is erected are of medium size, subturbinate, with a slightly elevated spire, an obliquely truncated subconical base, and a sinus in the periphery.

A rather acute peripheral angle separates the whorl profile into two very unequal parts: 1. The whorl above the periphery is slightly raised over a narrow suture from which the surface slopes gently before rising again toward a low, comparatively wide, and obtuse revolving salient situated midway between the suture and the peripheral angle. Beyond the salient there is a steeper second incline with a subsequent rise which terminates in a prominent narrow and elevated carina, the latter being separated from the peripheral angle by a flat and narrow pseudo-selenizone. 2. In the lower and larger part of the whorl the profile is slightly concave just below the periphery but rapidly forms an arched convexity terminating at a point less than halfway to the base, where-from it recedes by a less arched curvature toward the columella.

Above the periphery the margin of the outer lip is almost radial from the suture to the middle revolving salient at which it sharply turns with a sickle-shaped backward obliquity toward the carina on top of which it produces a V-shaped sinus, the outer and much shorter limb of which passes nearly straight across the narrow pseudo-selenizone without forming lunulae or parallel sides between the carina and the peripheral angle (Pl. 121, figs. 8 and 9). Below the periphery the outer lip is oriented obliquely backward and produces two consecutive shallow curvatures, each being a mirror image (enantiomorph) of an S. The upper curvature extends down from the peripheral angle midway to the base, and the lower one, similar but even less sinuous, from that point to the semilunar ridge about the umbilicus, into which it merges.

The columellar lip is arcuate, thickened, reflexed, and unchanneled. The presence or absence of the seemingly false umbilicus, and the size of the umbilical depression depend on the individual relation between the columellar inductura and the elevated semilunar ridge which extends from the base of the columella around the umbilical region. In some specimens there is a deep pit between the inner lip and the semilunar ridge in the bottom of which is a minutely phaneromphalous umbilicus (Pl. 121, fig. 6); in others, however, the columellar inductura completely fills the pit with callus leaving a barely perceptible fissure at its contact with the semilunar ridge (Pl. 121, fig. 4). The thin parietal inductura is present only in the lower part of the parietal wall. It merges with the columellar lip.

In the largest specimens there is an appreciable increase in the sutural dip between the penultimate and the last whorl. This change results in the gradually developed vertical wall below the peripheral angle of the penultimate whorl (Pl. 121, figs. 1 and 3).

Arizonella resembles *Büchelia* Schlüter from the *Stringocephalus* zone of the German Middle Devonian (Knight, 1941, p. 62, Pl. 20, figs. 2a–b). However, *Büchelia* is distinguished by the following characteristics: 1. A channeled inner lip; 2. A true selenizone on the periphery; 3. A narrow

revolving groove on the inner side of the selenizone instead of an elevated carina; 4. A whorl profile slightly arched and smooth above the periphery without a well defined revolving salient in the middle.

ARIZONELLA ALLECTA Stoyanow, n. sp.
Plate 121, figures 1–10

This species is established on four syntypes illustrated in this paper and twenty five metatypes in my collection. In all studied examples there is no deviation from the above generic diagnosis except for the difference in the degree of preservation.

Type.—Syntypes: Nos. IMB.13–IMB.16.

ARASTRA Stoyanow, n. gen.

Genotype, *Arastra torquata* Stoyanow, n. sp.

Small trochiform to subturbinate gastropods in which the outer lip is increasingly convex between the upper suture and the periphery but produces at the peripheral angle a short sinus with a slit thus giving rise to a distinctly bordered selenizone with shallow lunulae and, after a short forward swing, continues from the selenizone to the umbilical depression as an enantiomorphic S. The whorl profile slopes gently toward the periphery and broadly rounds below to the base. The whorl section is obtusely trapezoidal and the aperture varies from round to transversely oval. The contact between the periphery and the suture is linear in the younger stages, gradually it becomes undulating, with further growth the undulating projections develop frills which overlap the lower sutures, and in the advanced whorls such frills thicken into rather ill-defined tuberculiform prominences. The upper surface of the whorls is smooth in the earlier stages except for the lines of growth which mark the course of the outer lip, but with further development more rugged transverse increments occur on the growth lines. The collumellar lip is thick and reflexed. The thin parietal inductura is developed only in the lower part of the parietal wall and is in close contact or probably completely merges with the columellar lip. The umbilical depression is partly bordered by a more or less pronounced semilunar ridge which extends from the basal portion of the columellar lip. The minutely phaneromphalous umbilicus is tortuous within the shell.

Arastra, as has been pointed out to me by Dr. J. Brookes Knight in correspondence, shows certain resemblance to *Orecopia* Knight (1945, p. 586, Pl. 80, figs. 1a–1g). This is true especially regarding the trochiform representatives of that genus. The principal difference seems to be in the nature of the outer lip. In *Orecopia mccoyi* (Walcott), the genotype, and in two species from the Devonian of Russia originally placed by Keyserling in *Platyschisma* McCoy but which, as Dr. Knight has shown, most probably also belong in *Orecopia*, the outer lip forms a sinus on the upper surface of the whorl above the periphery and a tongue-shaped convexity at the peripheral angle (Knight, 1945, Pl. 80, figs 1b and 1c; Tschernyschew, 1887, Pl. 5, figs. 1a, 2a, and 4a); in *Arastra*, on the other hand, this relation is completely reversed. The development of frills in the advanced whorls of this genus also is distinctive.

ARASTRA TORQUATA Stoyanow, n. sp.
Plate 121, figures 11–29

This species is based on twelve syntypes illustrated in this paper and about one hundred metatypes of my collection. All studied specimens are silicifications of various degrees of preservation but the presence of diagnostic features has been established in all examples.

As is seen in the smallest illustrated specimen, the syntype No. IMB.17 (Pl. 121, figs. 11 and 12), in the first four observable whorls the outer lip appears below the upper suture as a fine, slightly raised, straight and backwardly directed obliquity not reaching the peripheral angle. This is because at this stage of development the growth lines abut against revolving "groove" and "lira" demarcating the upper border of a band-like selenizone on which the sinus is not identifiable. In most of the specimens the contact between the peripheral angle and the suture is a simple linear curve at this stage. Late on the fourth whorl the margin of the outer lip turns backward more noticeably as it approaches the periphery. On the fifth whorl it distinctly forms an enantiomorph of S above the periphery, a shallow crescentic sinus on the peripheral angle, and

a shallow enantiomorphic S on the lower surface of the whorl. Simultaneously the first frills appear (in some specimens the change from linear to undulating and even frilled periphery begins as early as in the fourth and even the third whorl, Pl. 121, figs. 14 and 15). It is in the earliest whorls, therefore, that a similarity between *Arastra torquata* and the species falling within *Orecopia* Knight is greatest. At such early growth stages the general resemblance between *A. torquata* and such species as "*Platyschisma*" *uchtensis* Keyserling is closest but the course of the outer lip is different. In addition, the revolving groove above the periphery of *Orecopia mccoyi* (Walcott) and of Keyserling's species appears to be morphologically distinct since these gastropods have no selenizone (Knight, 1945, Pl. 80, figs. 1a–1g; Tschernyschew, 1887, Pl. 5, figs. 4a–c). This interpretation is further supported by the inconstant nature of the upper border of the selenizone in *A. torquata* in which, through the irregular increment of shelly matter, the "lira" often encroaches upon the "groove," and in advanced whorls both are often missing altogether. Frills are absent in *Orecopia* and "*Platyschisma*" of Keyserling, and with the development of the frills the resemblance between *A. torquata* and those forms disappears.

With the further increment of shelly matter on the lines of growth in the advanced stages of *A. torquata* the outer lip becomes backwardly sickle-shaped above the selenizone (Pl. 121, figs. 16 and 25). When in the mature whorls the revolving increment above the selenizone is considerable, the whorl appears slightly concave above the peripheral angle (Pl. 121, fig. 27). In the last whorl of larger specimens the frills frequently are split spirally, and in such cases they appear underlined by undulating lappets (Pl. 121, fig. 27).

In the syntype No. IMB. 23 (Pl. 121, fig. 22), the spire has been removed to show the acute upper margin of the whorl. The formation of the sinus and the selenizone is illustrated in figures 16, 24, 25, and 27 of Plate 121. Figure 18 of the same plate shows the umbilical depression between the well developed semilunar ridge and the columellar lip.

Type.—Syntypes: Nos. IMB.17–IMB. 28.

All described specimens are in the paleontological collections at the University of Arizona.

REFERENCES

ANDRUSOV, N., 1897, Fossile und lebende Dreissensidae Eurasiens, Russian text pp. 1–687, German résumé pp. 1–115, and atlas in 4°, 20 plates. St. Petersburg.

DAVIES, A. MORLEY, 1935, Tertiary faunas, a text-book for oilfield palaeontologists and students of geology. Vol. 1, The composition of Tertiary faunas, 406 pages, 565 figures: Nordeman Publishing Company. New York.

KING, WILLIAM, 1850, A monograph of the Permian fossils of England, 258 pages, 29 plates. The Palaeontographical Society. London.

KNIGHT, J. BROOKES, 1941, Paleozoic gastropod genotypes: Geol. Soc. America, Special Papers, 32, 510 pages, 96 plates.

——, 1945, Some new genera of Paleozoic gastropods: Jour. Paleontology, Vol. 19, No. 6, pp. 573–587, pls. 79–80.

NEWELL, NORMAN D., 1942, Late Paleozoic Pelecypods: Mytilacea: State Geological Survey of Kansas, Vol. 10, Pt. 2, 115 pages, 15 plates, 22 figures. Lawrence.

STEPHENSON, LLOYD WILLIAM, 1941, The larger invertebrate fossils of the Navarro group of Texas: The University of Texas Publication No. 4101, 641 pages, 95 plates, 13 figures. Austin.

STOYANOW, A. A., 1936, Correlation of Arizona Paleozoic formations: Geol. Soc. America, Bull., Vol. 47, pp. 459–540, 1 plate, 5 figures.

STOYANOW, ALEXANDER, 1946, Molluscan faunule from Devonian Island Mesa beds, Arizona (Abstract): Geol. Soc. America, Bull., Vol. 57 No. 12, Pt. 2, p. 1234.

TSCHERNYSCHEW, TH., 1887, Die Fauna des mittleren und oberen Devon am West-Abhang des Urals: Mémoirs du Comité Géologique, T. 3, No. 3, Russian and German texts 208 pages, 14 plates. St. Pétersbourg.

ULRICH, E. O., 1893, New and little known Lamellibranchiata from the Lower Silurian rocks of Ohio and adjacent States: Report of the Geological Survey of Ohio, Vol. 7, Chapt. 7, pp. 627–693, pls. 45–56. Norwalk.

——, 1897, The Lower Silurian Lamellibranchiata of Minnesota: Final Report of the Geological and Natural History Survey of Minnesota, Vol. 3, Pt. 2, pp. 475–628, pls. 35–42, figs. 35–45. Minneapolis.

WILMARTH, M. G., 1938, Lexicon of geologic names of the United States: U. S. Geol. Survey, Bull. 896.

WOODS, HENRY, 1899–1903, A monograph of the Cretaceous lamellibranchia of England, Vol. 1, 232 pages, 42 plates, 7 figures: The Palaeontographical Society, London.

ZITTEL, KARL A., 1913, Text-Book of Paleontology adapted and edited by Charles R. Eastman, Vol. 1, 839 pages, 1594 figures: Macmillan and Co. London.

JOURNAL OF PALEONTOLOGY, VOL. 22, NO. 6, PP. 792–797, PL. 122, 1 TEXT FIG., NOVEMBER 1948

THE OSTRACODE GENUS *CYTHEREIS*

P. C. SYLVESTER-BRADLEY
University of Sheffield, England

ABSTRACT—A new subfamily is proposed to include the genus *Cythereis*. It consists of three related genera, characteristic of Jurassic, Cretaceous and Tertiary to Recent deposits respectively. Their genotypic species are described and figured. The evolution of the Cytheracea hinge is discussed, and three evolutionary trends recognized in the superfamily.

INTRODUCTION

TRIEBEL (1940) has shown that the genotype of *Cythereis* (a Cretaceous form) differs from most species which have been described from Tertiary deposits and Recent seas (see also Stephenson, 1947). It is here proposed that these later forms be separated from *Cythereis* as a distinct genus, for which *Trachyleberis* Brady 1898 seems to be the prior name. The evolution of the hinge in *Trachyleberis* has proceeded further than in *Cythereis*.

Middle Jurassic (Bathonian) species described in this paper show an earlier stage of hinge evolution than *Cythereis* and the new genus *Oligocythereis* is proposed for their reception.

The three sub-genera are distinguished, therefore, by their hinge characters, as described below. The subfamily Trachyleberinae is proposed for their reception.

TERMINOLOGY

Certain of the terms used in the following descriptions seldom appear in American paleontological literature. The definitions given below are more fully explained in the author's previous paper (S-Bradley, 1941).

Selvage (German "Saum"): A projection of the duplicature serving to seal the valves, especially prominent along the ventral margin. The selvage is an essential part of the shell structure of all Podocopa.

Flange (German "Aussenleiste"): A projection of the duplicature outside the selvage.

List (German "Innenleiste"): A projection of the duplicature inside the selvage,

EXPLANATION OF PLATE 122

FIGS. *1–6*—*Oligocythereis fullonica* (Jones and Sherborn). Left and right valves: *1*, *2*, dorsal views; *3*, *4*, external lateral views; *5*, *6*, internal lateral views. *1*, *3*, *5*, Brit. Mus. No. In. 42066; length, 0.61 mm.; height, 0.30 mm.; width, 0.16 mm. *2*, *4*, *6*, Brit. Mus. No. In. 42067; length, 0.57, mm.; height, 0.29 mm.; width, 0.16 mm. (p. 796)

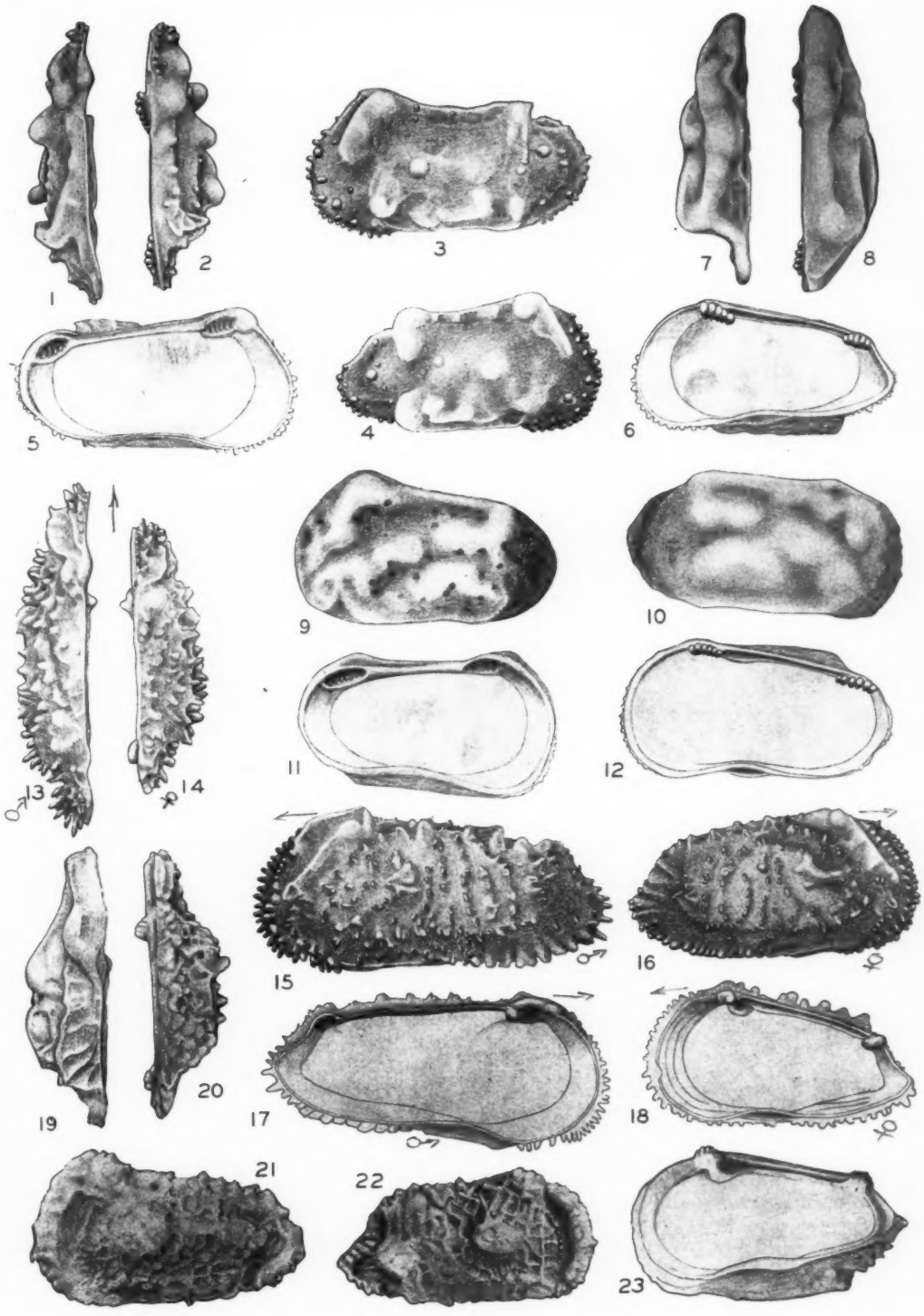
7–12—*Oligocythereis woodwardi* S-Bradley, n. sp. Left and right valves: *7*, *8*, dorsal views; *9*, *10*, external lateral views; *11*, *12*, internal lateral views. *7*, *9*, *11*, Brit. Mus. No. In. 42068 (paratype); length, 0.55 mm.; height, 0.33 mm.; width, 0.14 mm. *8*, *10*, *12*, Brit. Mus. No. In. 42069 (holotype); length, 0.58 mm.; height, 0.29 mm.; width, 0.17 mm. *Note.* Details of anterior duplicature in fig. *12* obscured by matrix. (p. 796)

13–18—*Trachyleberis scabrocuneata* (Brady). Left valve male, right valve female: *13*, *14*, dorsal views; *15*, *16*, external lateral views; *17*, *18*, internal lateral views. *13*, *15*, *17*, Brit. Mus. (Zool. Dept.) No. 1948.3.10.1; length, 1.10 mm.; height, 0.53 mm.; width, 0.24 mm. *14*, *18*, Brit. Mus. No. 1948.3.10.4; length, 0.91 mm.; height, 0.42 mm.; width, 0.22 mm. *16*, Brit. Mus. No. 1948.3.10.5; length, 0.93 mm.; height, 0.47 mm.; width, 0.23 mm. (Dimensions do not include spines.) (p. 794)

19, *23*—*Cythereis senckenbergi* Triebel. Female. *19*, left valve, dorsal view; *23*, right valve internal lateral view. *19*, Senckenberg Mus. No. XE 520; length, 0.86 mm.; width, 0.28 mm. *23*, Senckenberg Mus. N. XE 521; length, 0.88 mm.; height, 0.48 mm. (p. 795)

20–22—*Cythereis ornatissima* (Reuss). Female. *20*, right valve, dorsal view; *21*, *22*, left and right valves, external lateral views. *20*, Senckenberg Mus. No. XE 516; length, 0.86 mm.; width, 0.29 mm. *21*, *22*, Senckenberg Mus. No. XE 515. *21*, length, 0.86 mm.; height, 0.49 mm. *22*, length, 0.84 mm.; height, 0.43 mm. (p. 795)

(Figures *19–21* redrawn after Triebel; remainder original.)



Sylvester-Bradley, Ostracode genus *Cythereis*

usually not present in the Cytheracea, but prominent in certain genera of the Cypracea.

Flange groove: A groove developed between selvage and flange, particularly obvious in the central portion of the ventral margin of the right valve in Cytheracea.

Selvage groove: A groove developed between selvage and list.

Septa: Ridges developed on the inner lamella between selvage and inner margin.

Vestibule (German "Schalenhohlraum"): The space developed between outer and inner lamellae when the line of concrescence and inner margin do not coincide.

Accommodation groove: (German "Ausweichsfurche"): A groove developed above the median element of the hinge in the left valve of some Cytheracea, serving to accommodate the dorsal margin of the right valve when the carapace is open.

SYSTEMATIC PALEONTOLOGY

Family TRACHYLEBERIDAE Sylvester-Bradley n. fam.

Type genus: Trachyleberis Brady, 1898.

Diagnosis.—Cytheracea with accommodation groove lacking or reduced to a narrow shelf; straight hinge, with subdivided median element; and compressed carapace (especially anteriorly and posteriorly) though sometimes with alae.

Comprising the following genera:

Trachyleberis Brady, 1898.
Cythereis Jones, 1850.
Hemicythere Sars, 1925.
Pseudocythereis Skogsberg, 1928.
Procythereis Skogsberg, 1928.
Pterygocythereis Blake, 1933.
Buntonia Howe, 1935.
Favella Coryell and Fields, 1937.
Eucythereis Klie, 1940.
Isocythereis Triebel, 1940.
Platycythereis Triebel, 1940.
Anticythereis van den Bold, 1946.
Oligocythereis S-Bradley, nov.

The logical name for this family would be "Cythereidae," with *Cythereis* as the type genus, if there were not already so many family and subfamily names prefixed "Cyther-" (including Cytherinae, Cytheridae, Cytherideinae, Cytherideidae etc.). The author feels that less confusion will be caused by selecting *Trachyleberis* as the typical genus.

Cythereis has hitherto been placed in the subfamily Cytherinae. It differs fundamentally from *Cythere*, and does not, in the author's opinion, even belong to the family Cytheridae. Skogsberg (1928) has indicated that on neontological characters also the two genera cannot be considered as nearly related.

Subfamily TRACHYLEBERINAE Sylvester Bradley n. subfam.

Cythereis auctorum.

Diagnosis.—Ornate Trachyleberidae, with compressed subrectangular shell, pronounced muscle scar node (="subcentral tubercle"; forms a "muscle scar pit" when viewed from the interior; eye tubercle, posterior and anterior cardinal angles, and

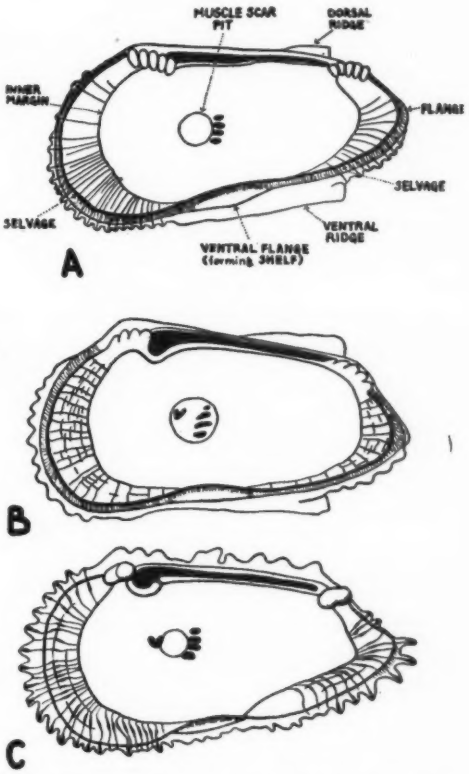


FIG. *1a–c*—Diagrams, based on the genotypes, showing the inside of the right valve of (A) *Oligocythereis*, (B) *Cythereis*, and (C) *Trachyleberis*. (A) and (C) original; (B) after Triebel, with modifications.

posterior and anterior marginal rims. Accommodation groove absent, or present only as a very narrow shelf. No vestibule. Median element of hinge subdivided, smooth or finely denticulate.

Remarks.—The subfamily should be restricted to those species of the Trachyleberidae which possess the basic ornament and shape given in the diagnosis.

Description.—Sexual dimorphy often apparent, the males longer in proportion than the females. Duplicature fairly broad, at the anterior about one-third the height of the carapace. Radial pore canals straight, crowded, often terminating in a marginal spine. Normal pore canals few, large, scattered. Ventral flange in right valve often pronounced, but well below the selvage, forming a "ventral flange shelf" rather than a flange groove.

Genus TRACHYLEBERIS Brady, emend.

Cythereis auctorum.

Trachyleberis, Brady, 1898.

Genotype: *Cythere scabrocuneata* Brady, 1880

Diagnosis.—*Trachyleberinae* in which anterior and posterior hinge elements are non-denticulate, strongly projecting teeth in the right valve, and in which the median element is a narrow bar, smooth or finely crenulate, with, at its anterior end, attached but below it, a rounded strongly projecting tooth.

Remarks.—To this genus belong most ornate species hitherto assigned to *Cythereis* from Tertiary rocks and Recent seas.

TRACHYLEBERIS SCABROCUNEATA (Brady)
Plate 122, figures 13–18

Cythere scabrocuneata, Brady, 1880 (part).
? Cythere dorsoserrata, Brady, 1880.
Cythere scabrocuneata, Brady and Norman, 1889 (part).
Trachyleberis scabrocuneata, Brady, 1898 (part).
? Cythereis dorsoserrata, Müller, 1912.

Description.—Strongly dimorphic, the males much longer than the females. Usual subrectangular shape, with triangular, much compressed posterior. Ornament of long, pointed spines, arranged in approximately transverse lines in the posterodorsal half of the carapace, but these lines become concentric with the muscle scar node in the anteroventral region, and longitudinal along the venter. Long, perforate marginal spines decorate both anterior and posterior. The eye tubercle is prominent, and its smooth shining surface stands out clearly. A sharp antero-dorsal ridge represents the antero-dorsal complex, and the line of this ridge is continued by a row of spines forming the anteroventral complex and ventral ridge. An elevated region, covered with spines, extends backwards from the muscle scar node. This *median complex* (not developed in *O. fullonica*, and therefore not mentioned in the analysis of the ornament of that species given in S-Bradley, 1948) is noted by Triebel as characteristic also in *Cythereis* (the "mittelrippe"). The muscle scar pit can be seen clearly from the inside. The corresponding node is also clear on the outside in slightly worn specimens; the prominent spines of the ornament tend to obscure it in unworn specimens.

The duplicature is as for the genus. The flange is not as distinct as in some species, its place being taken by a row of marginal spines. Radial pore canals thin and thread-like, widening slightly about the middle, irregularly spaced, crowded towards the venter (numbering forty to fifty in the anterior duplicature), slightly sinuous. Marginal spines perforated by wide pores. The ventral flange of the right valve makes an inconspicuous ridge well below the selvage, and is dwarfed by the prominent rows of ornamental spines immediately outside it.

The adductor muscle scar consists of four elongated scars disposed vertically above each other on the posterior margin of the muscle scar pit, with one V-shaped scar, opening upwards, in front of them, on the anterior margin of the pit.

The anterior hinge tooth of the right valve consists of an elevated base from the posterior end of which springs a peg-like projection. The posterior tooth is a rounded, oval projection, slightly elongated in a direction parallel to the length of the shell. This posterior tooth is indistinctly divided into three lobes, two anterior lobes, one above the other, and one smaller posterior lobe. The median bar of the left valve is very finely crenulate. The projecting tooth which forms the anterior subdivision of the median element of the left valve is prominent and peg-

like. In dorsal view it is seen to be sharply truncated by the socket at its anterior end; it slopes rather sharply down to the bar at its posterior end.

Remarks.—The description of the shell given above is based on an examination of five paratype specimens (single valves) from the "Challenger" collection, Station 233 B, Inland Sea, Japan, at 14 fathoms (lat. 34° 20′ N.; long. 133° 35′ E.), made available by the courtesy of Dr. J. P. Harding, of the British Museum.

Of the material identified by Brady and Norman (1889) with this species, I have examined the specimens collected by the "Valorous" expedition, and these are not of the same species as the genotype. It seems probable that Brady and Norman were mistaken in their supposition that, if the spines of the ornament were "rubbed away," the surface would be "found to be reticulated, being sculptured with round or hexagonal cells."

Genus CYTHEREIS Jones, 1850

Cythere (*Cythereis*), Jones, 1850 (part).
Cythereis, Triebel, 1940.

Genotype: *Cytherina ciliata* Reuss, 1845.

Diagnosis. Trachyleberinae in which anterior and posterior hinge elements are denticulate, and median element is clearly subdivided: in the right valve into an anterior rounded socket connected above and behind to a long narrow groove; in the left valve into a projecting rounded tooth connected above and behind to a long, smooth, projecting bar.

Description.—The genus has been fully and admirably described by Triebel (1940), but as this publication is not everywhere easy of access, drawings from his remarkable photographs are reproduced on Pl. 122 as figs. 19–23. The anterior tooth of the right valve is prominent and peg-like, but clearly denticulate. The posterior tooth is longer, distinctly denticulate, and not dissimilar to the posterior tooth of *Brachycythere*.

Remarks.—The genus is characteristic of the Lower Cretaceous; in the Upper Cretaceous it is accompanied by forms transitional to *Trachyleberis*. Possibly another generic name should be applied to forms with an entire anterior hinge element, but denticulate posterior.

CYTHEREIS ORNATISSIMA (Reuss)
Plate 122, figures 20–22

Cytherina ornatissima, Reuss, 1845.
? Cytherina ciliata, Reuss, 1845.
Cythereis ornatissima, Triebel, 1940.

This species was assumed by Jones and Hinde (1890), on Bosquet's recommendation, and apparently with Reuss's concurrence, to be synonymous with *C. ciliata* (Reuss), the genotype (see S-Bradley, 1947). Bearing in mind the greater requirement that exists nowaday in the distinction of species, the type of *C. ciliata* needs redescribing before its identification with *C. ornatissima* can be accepted.

C. ornatissima is an Upper Cretaceous (Turonian) species, and Triebel (1940) after an examination of topotype and metatype material has demonstrated that the anterior hinge element is denticulate, contrary to the description given by Alexander (1933). The illustrations are after Triebel, 1940.

CYTHEREIS SENCKENBERGI Triebel
Plate 122, figures 19, 23

Cythereis senckenbergi, Triebel, 1940.

This is a Lower Cretaceous (Neocomian) species close to *C. ornatissima*. The illustrations are after Triebel, 1940.

Genus OLIGOCYTHEREIS Sylvester-Bradley, n. gen.

Genotype: *Cythereis fullonica* Jones and Sherborn, 1888

Diagnosis.—Trachyleberinae in which the anterior and posterior hinge elements consist of groups of five or six toothlets in the right valve, and with median element a smooth groove in the right valve, wider at the anterior end, the subdivision more or less abrupt.

Description.—Duplicature, pore canals and basic ornament as described for subfamily. I have not yet come across any Jurassic specimens in which the muscle scars are clearly discernible. In one right valve of *O. woodwardi* four oblong scars were seen obscurely on the posterior edge of the muscle scar pit, but no anterior scar could be made out.

Remarks.—Species of this genus have so far only been found in Middle Jurassic beds.

The genus *Paracythereis* Jennings, 1936

(a homonym; not *Paracythereis* Delachaux 1928, nor *Paracytheris* Elofson, 1941) presents certain similarities to *Oligocythereis* (though its median element is crenulate). The genotypic species (*P. typicalis* Jennings, 1936), however, may well be a young molt of the form found in the same beds which Jennings refers to *Cythereis bassleri* Ulrich. *C. bassleri* var. *lata* Jennings of the same paper is probably the female of the same species. Le Roy (1945) has shown that early ontogenetic molts of two species of "*Cythereis*" (=*Trachyleberis*) have an "*Archycythereis*" type of hinge. If I am right in assuming that "*Paracytheris*" *typicalis* is an early molt of *Trachyleberis bassleri*, it presents an even better case of palingenesis than Le Roy's ontogenies.

OLIGOCYTHEREIS FULLONICA (Jones and Sherborn)
Plate 122, figures 1–6

Cythereis fullonica, Jones and Sherborn, 1888.
Cythereis fullonica, S-Bradley, 1948, (part).

Description.—Carapace subrectangular. Posterior rounded or triangular. The eye tubercle continuous with the sharp, straight ridge of the anterodorsal complex, which extends towards the anterior margin to a point near the center line of the carapace. The muscle scar node is prominent and distinct. In front of and below it an anteroventral complex runs into the ventral ridge, which is terminated posteriorly by a swelling—the posteroventral complex. Above the ventral ridge and between anteroventral and posteroventral complexes there is a series of swellings of characteristic shape. The posterodorsal complex is a high ridge projecting conspicuously over the dorsal margin, and extending vertically down the carapace to about the center line without branching. The dorsal ridge is narrow and high, connecting antero- and postero-dorsal complexes. A posterior hinge tubercle is visible at the cardinal angle behind the posterodorsal complex. Both marginal rims are ornamented with tubercles and short spines.

The subdivision of the median element of the hinge is very slight. The anterior end of the median bar in the left valve is more prominent than its posterior portion.

Remarks.—The plesiotypes are from the author's Bed No. 47 FW 9, at the top of the economic Fuller's Earth (Bathonian), mined near Combe Hay, Bath, England.

OLIGOCYTHEREIS WOODWARDI Sylvester-Bradley, n. sp.
Plate 122, figures 7–12

Description.—The carapace is much smoother than in *O. fullonica*. The posterodorsal complex divides into two widely splayed branches. The muscle scar node extends into the posteroventral complex, and is connected to the anteroventral complex. The ventral ridge is ill defined. The eye tubercle is connected to a rounded prominence forming the anterodorsal complex. The anterior and posterior margins are not spinous, and are but slightly tuberculate.

The median groove of the hinge of the right valve is clearly subdivided, the anterior portion shorter and wider than the posterior. In the left valve the eye tubercle makes a prominent swelling in front of the hinge socket.

Remarks.—The holotype and paratype (figured on Pl. 122), are from the same locality and bed as the plesiotypes of *O. fullonica*.

THE EVOLUTION OF THE CYTHERACEA HINGE

During the course of his study of Middle Jurassic Ostracoda(still proceeding), the author has discovered intermediate stages in the development of the *Brachycythere* type of hinge. The genus *Progonocythere* Sylvester-Bradley (see Sylvester-Bradley, 1948) has reached a stage comparable to *Oligocythereis*. In this case, however, the median element is at first denticulate. It is still a matter for conjecture whether the early Trachyleberinae had a denticulate median element. Alexander (1934) has shown that in *Loxoconcha* the median element is smooth in Cretaceous species, but became denticulate during Tertiary times. This is paralleled by the finely crenulate bar in *Trachyleberis scabrocuneata*. It is clear that there are three important evolutionary trends in the development of the Cytheracea hinge:

(1) The acquisition, from a primitively smooth hinge, of crenulations in all three elements, such crenulations increasing in strength in early evolutionary series to form separate toothlets, and coalescing in later

evolutionary stages until they revert to a smooth phase;

(2) The subdivision of the median element;

(3) The development of secondary crenulations on the median bar.

ACKNOWLEDGMENTS

The drawings for the plate were prepared by Miss D. Robinson from camera lucida sketches by the author. The artist's fees were in part met by the Government Grants Committee of the Royal Society, London, England.

The author wishes to thank Dr. J. P. Harding and the authorities of the British Museum for their constant courtesy and help.

REFERENCES

ALEXANDER, C. I., 1933, Shell Structure of the Ostracode genus *Cytheropteron* and species from the Cretaceous of Texas: Jour. Paleontology, vol. 7.

——, 1934, Ostracoda of the Midway (Eocene) of Texas: Jour. Paleontology, vol. 8.

BRADY, G. S., 1880, Report on the Ostracoda dredged by H.M.S. Challenger during the years 1873–1876: Rept. Sci. Results of Voyage of H.M.S. Challenger, Zool., vol. 1.

——, 1898, On new or imperfectly known species of Ostracoda, chiefly from New Zealand: Zool. Soc. London, Trans., vol. 14.

——, and A. M. NORMAN, 1889. Monograph of the Marine and Freshwater Ostracoda of the North Atlantic and of N.W. Europe. Sec. 1, Podocopa: R. Dublin Soc., Sci. Trans., ser. 2, vol. 4.

JENNINGS, P. H., 1936, A microfauna from the Monmouth and Basal Rancocas groups of New Jersey: Bull. Amer. Paleontology, vol. 23, No. 78.

JONES, T. R., 1850, Monograph of the Entomostraca of the Cretaceous Formation of England. Palaeont. Society, 1849 (1850).

——, and G. J. HINDE, 1890, Supplementary Monograph of the Cretaceous Entomostraca of England and Ireland: Pal. Society, 1890.

——, and C. D. SHERBORN, 1888, On some Ostracoda from the Fuller's-Earth Oolite and Bradford Clay: Bath Nat. Hist. and Antiq. Fld. Club, Proc., vol. 6.

LEROY, L. W., 1945. A Contribution to Ostracodal Ontogeny: Jour. Paleontology, vol. 19.

MÜLLER, G. W., 1912. Ostracoda: Das Tierreich. Lief. 31. Berlin.

REUSS, A. E., 1845, Die Versteinerungen der Böhmische Kreideformation. Stuttgart.

SKOGSBERG, T., 1928, Studies on Marine Ostracods. Part 2. External Morphology of the Genus *Cythereis* with descriptions of 21 new sp. California Acad. Sci., Occ. Pap., 15.

STEPHENSON, M. B., 1947, Weches Ostracoda: Corrections. Jour. Paleontology, vol. 21.

SYLVESTER-BRADLEY, P. C., 1941, The Shell Structure of the Ostracoda and its Appication to their Palaeontological Investigation: Ann. and Mag. Nat. History, ser. 11, vol. 8.

——, 1947. Some Ostracod Genotypes: Ann. and Mag. Nat. History, ser. 11, vol. 13.

——, 1948, Bathonian Ostracoda from the Bouet Bed of Langton Herring, Dorset: Geol. Mag. vol. 85.

TRIEBEL, E., 1940, Die Ostracoden der Deutschen Kreide. Cytherideimae und Cytherinae aus der Unteren Kreide: Senckenbergiana, vol. 22.

JOURNAL OF PALEONTOLOGY, VOL. 22, NO. 6, PP. 798–803, PL. 123, NOVEMBER 1948

UPPER CAMBRIAN TRILOBITES FROM OKLAHOMA

E. A. FREDERICKSON
University of Oklahoma, Norman, Oklahoma

ABSTRACT—One new genus and three new species are described from the *Elvinia* zone of the Honey Creek formation in the Arbuckle and Wichita Mountains, Oklahoma. In addition, a revision is made of ten species of *Elvinia* zone trilobites previously described.

I had intended to include the following descriptions in a more complete report on the Honey Creek fauna of Oklahoma, but a fellow worker has requested their publication in order that these species might be referred to in a faunal and stratigraphic paper now ready for publication.

The specimens described below are in the Oklahoma Geological Museum (O.G.M.). The localities referred to are as follows:

Locality 8. NE. ¼ NE. ¼ Sec. 2, T. 4 N., R. 13 W., old W.P.A. quarry, Blue Creek Canyon, Wichita Mts., Comanche County, Okla.
Locality 11. SE. ¼ SE. ¼ Sec. 4, T. 1 S., R. 1 W., northwest edge West Timbered Hills, Arbuckle Mts., Murray County, Okla
Locality 12. NE. ¼ NW. ¼ Sec. 9, T. 1 S., R. 1 W., one-half mile southeast of Loc. 11.
Locality 13. SW. ¼ SE. ¼ Sec. 4, T. 1 S., R. 1W., one-quarter mile west of Loc. 11.
Locality 14. SE. ¼ SE. ¼ Sec. 23, T. 1 S., R. 1 W., south edge West Timbered Hills, Murray County, Okla.

SYSTEMATIC DESCRIPTIONS

Genus CAMARASPIS Ulrich and Resser, 1924

The genus *Camaraspis* was founded on the species *Arionellus convexus* Whitfield in an unpublished manuscript prepared by Ulrich and Resser and referred to by E. O. Ulrich in a paper presented before the Wisconsin Academy of Sciences in 1924.

Since that date *Camaraspis* has been referred to repeatedly in publications on Upper Cambrian stratigraphy and paleontology in the United States. Inasmuch as Ulrich in founding the new genus merely proposed changing the name from *Arionellus convexus* Whitfield to *Camaraspis convexus* (Whitfield) Ulrich and Resser, I assume that the description of the type species was considered adequate for the genus.

Three species including *Camaraspis convexa* (Whitfield) occur in the Oklahoma collection. The specimens have been replaced by calcite and preserve minute surface markings whereas Whitfield's specimens are molds in friable sandstone and are poorly preserved. Although Whitfield did not mention the presence of a marginal furrow and border in his original description, he did show these structures in the illustration printed four years later. All three species of the genus found in Oklahoma show a very faint depression, scarcely visible in some specimens, dividing the pre-glabellar area of the cranidium into two parts; the border being about one-third the width of the brim.

CAMARASPIS CONVEXA (Whitfield)

Plate 123, figures 12, 13

Arionellus (Agraulos) convexus WHITFIELD, 1878, Wisconsin Geol. Survey, Ann. Rept. for 1877, p. 57.
Arionellus convexus WHITFIELD, 1882, Geol. Wisconsin, vol. 4, p. 190, pl. 1, fig. 17.
Agraulos convexus Whitfield MILLER, 1889, N. Am. Geology and Paleontology, p. 527.
Agraulos convexus Witfield VOGDES, 1890, U. S. Geol. Survey, Bull. 63, p. 90.
Agraulos hemisphericus BERKEY, 1898, Amer. Geologist, vol. 21, no. 5, p. 289, pl. 20. figs. 14, 15.
Agraulos cushingi RUEDEMANN, 1916, N. Y. S. Mus. Bull., no. 189, p. 89, pl. 30, figs. 1–4.
Plethopeltis arenicola RAYMOND, 1924, Proc. Boston Soc. Nat. Hist., vol. 37, no. 4, p. 416, pl. 13, fig. 1.
Plethopeltis hemispherica (Berkey) RAYMOND, 1924, Proc. Boston Soc. Nat. Hist., vol. 37,no. 4, p. 415.
Camaraspis convexus (Whitfield) ULRICH and RESSER Mss., Ulrich, 1924, Wisconsin Acad. of Sci., Arts and Letters, vol. 21, p. 94.
Camaraspis convexus (Whitfield) TWENHOFEL, RAASCH and THWAITES, 1935, Geol. Soc. of America Bull., vol. 46, p. 1703 (cited in faunal list).
Camaraspis convexus (Whitfield) RAASCH, 1939, Geol. Soc. of America Sp. Papers No. 19, p. 91, (cited in faunal list).

Camaraspis convexa (Whitfield) SHIMER and SHROCK, 1944, Index Fossils of Nor. Amer., p. 621, pl. 260, figs. 12–14.
(non) *Agraulus convexus* Whitfield BERKEY, 1898, idem., p. 288.
(non) *Agraulus convexus* Whitfield var. A. BERKEY, idem.
(non) *Agraulus convexus* Whitfield var. B. BERKEY, idem.

Original description:

Glabella and fixed cheeks united, strongly convex and somewhat paraboloid in form, length and width nearly equal; anterior margin of the head between the suture lines regularly and somewhat sharply arcuate; palpebral lobes small, not very prominent, situated posterior to the middle of the head. Glabella rather less than two-thirds of the entire length of the shield, rounded conical in form and somewhat abruptly tapering; scarcely defined at the margins by the dorsal furrows, and apparently very indistinctly marked by three pairs of oblique furrows; occipital ring narrower than the base of the glabella, and more prominent, and also extending beyond the posterior limits of the fixed cheeks; occipital furrow very shallow and faintly marked, the ring short in the middle and reduced to its minimum width at its junction with the dorsal furrows. Fixed cheeks, half as wide as the glabella; frontal limb as long in the middle as the width of the fixed cheek, and slightly increasing toward the lateral angles. Facial suture passing nearly direct from the eye to the anterior margin of the head, its direction posterior to the eye not determined. The largest example of the glabella and fixed cheeks observed, measures about three-fourths of an inch in length by nearly seven-eighths of an inch in width at the base. No other parts of the organism have been observed.

Remarks.—*C. convexa* is abundant throughout the lower portion of the Honey Creek formation and forms one of the best index fossils for this formation. The species is apparently widespread throughout equivalent beds in many parts of the central United States and has been reported from South Dakota, Wisconsin, Texas, Missouri, and Montana.

Occurrence.—Upper Cambrian, Honey Creek formation (*Elvinia* zone), Arbuckle and Wichita Mountains.

Hypotype.—Cranidia, O.G.M. 105-16F-11, locality 11.

CAMARASPIS PLANA Frederickson, n. sp.
Plate 123, figures 14, 15

Cranidium hemispherical, moderately convex axially; glabella poorly defined, slightly convergent, rounded anteriorly, raised slightly above fixed cheeks; two pairs of faint glabellar furrows on exfoliated specimens poorly visible on unpeeled surface; occipital furrow shallow, widening laterally and bifurcating into two shallow prongs; dorsal furrow shallow and faint. Brim and border convex, wide, continuous with smooth convex curve of glabella; poorly visible, wide, shallow furrow on exfoliated specimens forming marginal furrow; border poorly differentiated from brim. Fixed cheeks about one-half the width of glabella across eyes; palpebral lobes of moderate size, hemispherical, maintaining very slight transverse convexity of cranidium, located posterior to middle of head; slight flexure in cheek forming faint ocular ridge. Posterior limbs broadly triangular, sloping away from glabella and marked by wide, shallow marginal furrow. Free cheek unknown.

Facial suture cutting frontal margin at center and running outward to margin of frontal rim, then bending backwards and slightly inward to palpebral lobe around which it curves, thence backward and outward cutting posterior margin within genal angle.

Outer surface of test smooth.

Pygidium not known.

Remarks.—The three species of *Camaraspis* present in Oklahoma differ mainly in degree of convexity, although there are other minor differences. The convexity of the cranidium both in axial and transverse directions increases in degree from the slightly convex *C. plana* to the markedly convex *C. convexa* and ending with the very rotund *C. parabola*.

Occurrence.—Upper Cambrian, Honey Creek formation (*Elvinia* zone), Arbuckle and Wichita Mountains.

Holotype.—Cranidium, O.G.M. 104-16F-12, locality 12.

CAMARASPIS PARABOLA Frederickson, n. sp.
Plate 123, figures 16–19

Cranidium tumid, parabolic along axial line, less convex in transverse direction; glabella wide, convergent, rounded, swollen in posterior portion, scarcely defined by the dorsal furrow which is essentially absent anteriorly; no glabellar furrows; no occpital ring or furrow. Brim essentially continuous with front of glabella, about twice as wide

as the border which maintains the slope of the cranidium; marginal furrow consisting of a scarcely visible broad, shallow depression. Fixed cheeks about one-fourth the width of glabella, maintain glabellar convexity with no change of slope; palpebral lobe very slightly elevated, moderate in size, located posterior to middle of cranidium; no ocular ridge. Posterior limbs broadly triangular, convex and marked with shallow marginal furrow. Free cheek unknown.

Facial suture cutting frontal margin at center and trending laterally, then curving around frontal rim and slightly inward to and around palpebral lobes, thence outward and backward cutting posterior margin within genal angle.

Outer surface of test smooth.

Pygidium not known.

Remarks.—*C. parabola* is less abundant than the other two species of *Camaraspis* and has been found only in the Wichita Mountains. Distinguishing features are the greater convexity of the cranidium, poorly defined glabella and absence of the occipital furrow.

Occurrence.—Upper Cambrian, Honey Creek formation (*Elvinia* zone), Wichita Mountains.

Holotype.—Cranidium, O.G.M. 105-16F-43, locality 8.

Genus DOKIMOCEPHALUS Walcott

Description.—Cranidium of medium size, elongate; glabella convex, conical with broadly rounded front; three pairs of glabellar furrows which do not meet over glabella, anterior furrows faint, posterior pair deep, oblique; occipital furrow deep and oblique at sides, faint and straight over center of glabella, long occipital spine; dorsal furrow deep at sides, shallow in front of glabella. Brim convex, very narrow in front of glabella, expanded in front of palpebral lobes, separated from border by shallow marginal furrow; border very elongate, greatest width at marginal furrow, narrowing anteriorly very slightly to broad concave shovel-like extension, or markedly to form thick spine or spatulate process. Fixed cheeks narrow; palpebral lobes elevated, situated opposite posterior pair of glabellar furrows, marked by furrow; ocular ridge faint. Posterior limbs of medium width, triangular, with deep marginal furrows. Free cheek and pygidium unknown.

Outer surface of test finely granulose.

Remarks.—Walcott included two species, *D. pernasuta*, the genotype, and *D. gregori* in this genus. Resser, in 1942, described several new species of *Dokimocephalus* from the Honey Creek formation, but referred them to the genus *Burnetia*. Of these *B*

EXPLANATION OF PLATE 123

FIGS. 1–3—*Dokimocephalus lingula* (Resser). *1, 2*, Hypotype; poorly preserved cranidium showing occipital spine and large border, ×2, O. G. M. 105–16F–17, loc. 8. *3*, Hypotype, fragmental cranidium, ×2, O. G. M. 105–16F–19, loc. 12 (p. 801)

4–8—*Dokimocephalus curta* (Resser. *4, 5*, Hypotype; dorsal and profile views of a cranidium showing the spoon shaped character of the blunt anterior spine, ×2, O. G. M. 105–16F–21, loc. 12. *6*, Hypotype; cranidium, ×2, O. G. M. 105–16F–22, loc. 11. *7, 8*, Hypotype; dorsal and profile views of another cranidium showing the long occipital spine, ×2, O. G. M. 105–16F–18, loc. 11. (p. 801)

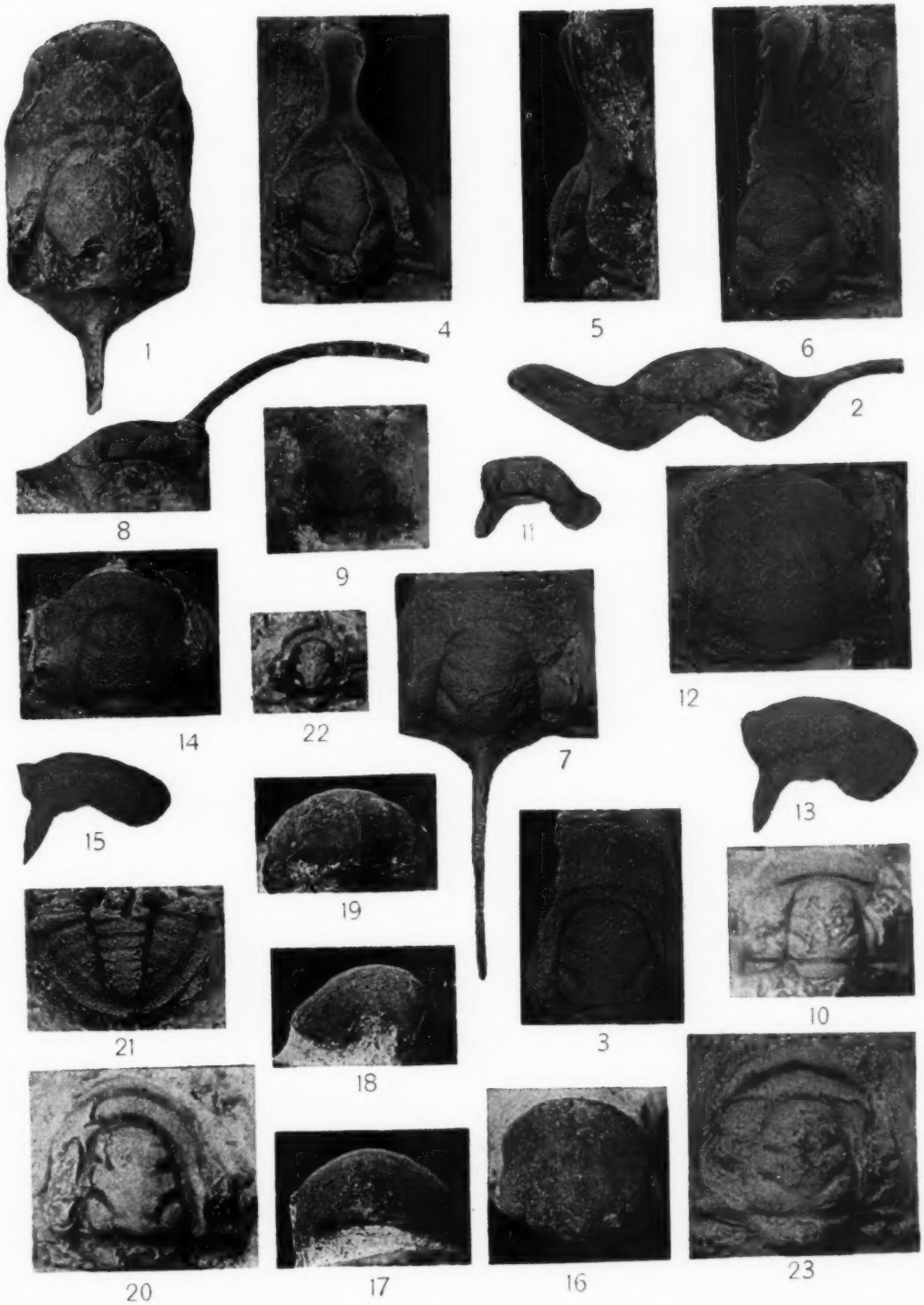
9–11—*Ptychopleurites amplooculatus* Frederickson, n. sp. *9*, Paratype; cranidium, ×6, O. G. M. 105–16F–14, loc. 15. *10, 11*, Holotype; dorsal and profile views of cranidium, ×6, O. G. M. 105–16F–15, loc. 13. (p. 803)

12, 13—*Camaraspis convexa* (Whitfield). Hypotype; dorsal and profile views of cranidium, ×2, O. G. M. 105–16F–11, loc. 12. (p. 798)

14, 15—*Camaraspis plana* Frederickson, n. sp. Holotype; cranidium, ×2, dorsal and profile views showing faint transverse furrow, O. G. M. 105–16F–12, loc. 12. (p. 799)

16–19—*Camaraspis parabola* Frederickson, n. sp. Holotype; cranidium, ×2, O. G. M. 105–16F–43, loc. 8. *16*, dorsal view; *17*, front view; *18*, profile view; *19*, posterior view. (p. 799)

20–23—*Kindbladia wichitaensis* (Resser). *20*, Hypotype, slightly deformed cranidium, ×4, O. G. M. 105–16F–4, loc. 8. *21*, Hypotype, pygidium, ×4, O. G. M. 105–16F–2, loc. 9. *22*, Hypotype, cranidium, ×4, O. G. M. 105–16F–4a, loc. 8. *23*, Hypotype, cranidium showing pits in marginal furrow, ×4, O. G. M. 105–16F–3, loc. 9. (p. 803)



Frederickson, Upper Cambrian trilobites

curta and *B. intermedia* are valid species of *Dokimocephalus*, and I consider *B. intermedia*, *B. extensa* and *B. lingula* to be conspecific. The genus as now constituted therefore, includes the following species:

D. pernasuta
D. gregori
D. curta
D. intermedia

DOKIMOCEPHALUS CURTA (Resser)
Plate 123, figures 4–8

Burnetia curta RESSER, 1942, Smithsonian Misc. Coll. vol. 103, no. 5, p. 83, pl. 17, figs. 28, 29.

Description.—Cranidium elongate, with a convex, broadly conical glabella; three pairs of glabellar furrows turn sharply backward, first two pair faint, posterior pair deeply impressed; occipital ring wide in center, narrow at sides with very long convex occipital spine; occipital furrow deep, oblique at sides, faint across center; dorsal furrow impressed but shallowing around front of glabella. Brim slightly convex, very narrow in front of glabella; marginal furrow shallow, narrow; border concave as a whole, elongate, extending forward as a long, narrow, spoon-shaped spatulate process, the sides of which round over into the ventral doublure. Fixed cheeks narrow, convex; palpebral lobes elevated, situated opposite midpoint of third pair glabellar furrows; palpebral furrow deep; well defined ocular ridge. Posterior limbs narrow, moderate in length, with deeply impressed furrow. Free cheek not known.

Facial suture cutting anterior margin at point where curvature of lateral margin of border changes from concave to convex, curving outward to marginal furrow, thence slightly inward to and around the palpebral lobes and then passing diagonally outward cutting posterior margin within genal angle.

Pygidium not known.

Outer surface of glabella finely granulose, granules becoming very minute on fixed cheeks, brim and border.

Remarks.—This species is very abundant in the Honey Creek formation. The length of an average cranidium is about 20 mm.; length including the occipital spine, about 40 mm. However, some incomplete cranidia probably attained a total length including the occipital spine of 80 mm. It is most unfortunate that Resser's specimens are so poor and inadequate. The holotype plainly shows a serrated edge where the elongate spatulate process was broken off, although the illustration of the holotype shows a smoothly trimmed border. Most of my specimens also have the border broken off near the marginal furrow, and it is unusual to fine one which retains the spoon-like border in its entirety.

Occurrence.—Upper Cambrian, Honey Creek formation (*Elvinia* zone), Arbuckle and Wichita Mountains.

Hypotypes.—Cranidium, O.G.M. 105-16F-22, locality 11; cranidium, O.G.M. 105-16F-21, locality 12; cranidium, O.G.M. 105-16F-18, locality 11.

DOKIMOCEPHALUS INTERMEDIA (Resser)
Plate 123, figures 1–3

Burnetia intermedia RESSER, 1942, Smithsonian Misc. Coll., vol. 103, No. 5, p. 80, pl. 17, figs. 10, 11.
Burnetia extensa RESSER, idem, (in part) p. 81, pl. 17, figs. 15, 16, 17, 18, 20.
Burnetia lingula RESSER, idem, p. 82, pl. 17, figs. 32, 33.

Description.—Cranidium with convex, very broadly conical glabella; three pairs of glabellar furrows bending sharply backward, posterior pair deeply impressed, others faint; occipital ring rounded triangular in shape, widest at center, occipital spine present; occipital furrow deep, oblique at sides, faint and straight over glabella; dorsal furrow impressed at sides, shallow around anterior portion of glabella. Brim very narrow anterior to glabella, convex; marginal furrow shallow, rounded; border concave, broad, equal in length to three-fifths distance from occipital furrow to front of glabella. Fixed cheeks narrow, convex; palpebral lobes situated opposite mid-point of oblique posterior pair of glabellar furrows elevated, distinct, with well defined furrow; ocular ridges present. Posterior limbs as in *D. curta*.

Facial suture cuts anterior margin on line with dorsal furrow, trends outward and backward in sigmoidal curve around marginal furrow, thence inward at small angle to palpebral lobes, around which it curves and then passing outward; further course unknown.

Pygidium not known.

Outer surface of test finely granulose; granules becoming smaller on border.

Remarks.—Only three cranidia of *D. intermedia* occur in my collection. The most complete cranidium is badly exfoliated (pl. 123, figs. 1 and 2) and does not show the specific characters as well as the other figured specimen (pl. 123, fig. 3). *Burnetia lingula* Resser is obviously conspecific with *D. intermedia* and agrees in every detail. Resser chose as the holotype of *Burnetia extensa* an incomplete specimen of *D. intermedia*. The holotype and paratypes of *B. extensa* herein assigned to *D. intermedia* plainly show the broken and fragmental border margins, whereas the trimmed photographs give the appearance of a blunt anterior spine. *B. extensa* Resser thus becomes a synonym of *D. intermedia*.

One specimen, illustrated as a paratype of the invalid species *B. extensa* (Resser, 1942, pl. 17, fig. 19) differs from *Dokimocephalus intermedia*. This form is very small and is similar in every detail to *D. intermedia* except in the character of the border which tapers gradually to a blunt spine. This is the only example of this type in either the National Museum Collections or in my own. The small size of the cranidium indicates that it might represent a young molt of *D. intermedia* and therefore may not be a valid species. Further detailed collecting may solve this problem. The pygidium illustrated by Resser in fig. 22, pl. 17 and assigned to *B. extensa* belongs to the genus *Elvinia*.

Occurrence.—Upper Cambrian, Honey Creek formation (*Elvinia* zone), Arbuckle and Wichita Mountains.

Hypotype.—Cranidium, O.G.M. 105-16F-19, locality 12: cranidium, O.G.M. 105-16F-17, locality 8.

Genus KINDBLADIA Frederickson, n. gen.

A number of new species from Oklahoma and Missouri were described by Resser, 1942, and assigned to the genus *Berkeia*. The following species, *B. retusa*, *B. angustata*, *B. wichitaensis*, *B. jucunda*, *B. missouriensis*, and *B. comes*, differ radically from the genotype *B. typica* Resser and are herein included in the new genus *Kindbladia*. Of these, I consider the following to be conspecific: *B. retusa* and *B. angustata;* and *B. wichitaensis*, *B. jucunda* and *B missouriensis*. Thus constituted, the genus *Kindbladia* consists of three species: *K. retusa*, *K. wichitaensis*, and *K. comes*. *Kindbladia* differs from *Berkeia* in having narrow, upsloping fixed cheeks, a more convex glabella which is faintly keeled on adult specimens, a pitted dorsal furrow anterior to the glabella, and a longer, narrower cranidium.

Description.—Cranidium elongate; glabella subconical, rounded at front, convexity moderate, faintly keeled along axis; three pairs of glabellar furrows which do not cross glabella, first pair faint, short, nearly straight, second and third pair distinct, arcuate, third pair deeply incised; occipital ring wider at center, usually bearing short occipital spine, occipital furrow curved and deepest at sides, widening and shallowing across center. Brim convex, sloping steeply down to marginal furrow; the furrow well defined, crescentic, with three oval pits, one on axial line and others on line with sides of glabella; pits not apparent on exfoliated specimens. Border convex, upturned, about one-half the width of brim at center and narrowing somewhat toward sides giving a pointed appearance. Fixed cheeks about one-third the width of glabella, upsloping to form short bow-like narrow ridges; palpebral lobes opposite glabellar midpoint, narrow, crescentic, located below ridge-like portions of fixed cheeks. Posterior limbs maintain convexity of cranidium laterally, length about one-half that of occipital ring. Free cheek not known.

Facial suture cuts frontal margin near center, curves posterolaterally to marginal furrow, then inward to palpebral lobe around which it curves and then outward and backward to posterior margin.

Glabellar surface finely granulose. Brim has fine raised lines running anteriorly.

Pygidium convex, rounded triangular in shape; axial lobe very convex, narrow, converging evenly to rounded termination at rear marginal border; five axial furrows and terminal portion, first three furrows well-marked; pleural lobes flatly convex, sloping away from axial lobe to flat upturned marginal border of medium width; pleural lobes marked by four shallow furrows.

Genotype: *Kindbladia wichitaensis* (Resser).

Occurrence.—Upper Cambrian, *Elvinia* zone, Oklahoma, Texas, Missouri known at present. Probably widespread.

KINDBLADIA WICHITAENSIS (Resser)
Plate 123, figures 20–23

This species is very abundant in the Honey Creek formation where it occurs ranging through much of the *Elvinia* zone. *K. wichitaensis* may be distinguished from *K. retusa* in that the glabella of the former appears sunken below the eye lobes as a result of the exceptionally deep dorsal furrow, thus giving a flatter appearance to the cranidium as a whole and to the glabella in particular.

Hypotype.—Cranidia, O.G.M. 105-16F-3; O.G.M. 105-16F-5, locality 9; O.G.M. 105–16F-2, locality 9.

Genus PTYCHOPLEURITES Kobayashi, 1936

PTYCHOPLEURITES AMPLOOCULATUS Frederickson, n. sp.
Plate 123, figures 9–11

Glabella convex, slightly convergent and rounded anteriorly; three pairs of weak, oblique glabellar furrows; occipital furrow deeply impressed at sides of glabella and becoming faint in front. Brim narrow; border convex, elevated in the middle and decreasing only slightly in width at the extremities. Fixed cheeks narrow but expanded widely at palpebral lobes which are elevated and elongate, extending from position anterior to second pair of glabellar furrows almost to occipital furrow; wide palpebral band separated from inner cheek by narrow furrow; faint ocular ridges present. Posterior limbs narrow, elongate, strap-like, with narrow, deep marginal furrows. Free cheek not known.

Facial suture cutting anterior margin at center, curving out around border, then converging to palpebral lobe around which it curves gently; thence sharply outward at nearly right angles to axial line and around posterior limb to posterior margin.

Average cranidium 3½ mm. long, 5 mm. wide across posterior limbs. Surface of test very minutely granular.

Remarks.—This species resembles *P. brevifrons* Kobayashi, the genotype, in all characters except the palpebral lobe and the posterior limbs. The posterior limbs of *P. brevifrons* illustrated by Kobayashi are much wider, and the palpebral lobes are considerably smaller and more anteriorly located than in *P. amplooculatus.*

Occurrence.—Upper Cambrian, Honey Creek formation (*Ptychopleurites* zone, associated with *Irvingella*), Arbuckle and Wichita Mountains, Oklahoma,

Holotype.—Cranidium, O.G.M. 105-16F-15, locality 13; paratype, cranidia, O.G.M. 105-16F-14, locality 14.

REFERENCE

RESSER, C. E., 1942, New Cambrian Trilobites: Smithsonian Misc. Coll., vol. 103, no. 5.

JOURNAL OF PALEONTOLOGY, VOL. 22, NO. 6, PP. 804–805, PL. 124, NOVEMBER 1948

A NEW *PECTEN* FROM THE UPPER MIOCENE OF CALIFORNIA

U. S. GRANT AND ROBERT E. STEVENSON

ABSTRACT—A new species of *Pecten* from the Neroly formation of the Upper Miocene of California, *Pecten* (*Pecten*) *juanensis*, is illustrated and described. The similarities between the new species and *Pecten coalingaensis* and *P. vogdesi* suggest a genetic relationship between the three forms with *P. juanensis* apparently being ancestral to the latter two species.

A number of years ago Mr. E. H. Quayle and the senior author made a collection of upper Miocene Mollusca and Echinoidea in the San Juan River area of eastern San Luis Obispo County, California. The collections consisted largely of Pectens and specimens of *Astrodapsis*, the latter being a common scutellid echinoid of the upper half of the Miocene and lower half of the Pliocene of California. The Pectens include *Lyropecten estrellanus* (Conrad) and a new species of typical *Pecten* belonging to the *Pecten coalingaensis* clan. A description of this new species follows, together with a discussion of its probable relationships.

PECTEN (PECTEN) JUANENSIS Grant and Stevenson, n. sp.

Shell of moderate size; right valve highly ventricose; left valve flattish (none well preserved); right valve sculptured with 18 to 21 rounded ribs which are less convex near their medial portions though not flat, with evenly rounded interspaces which are somewhat narrower than the ribs; no interribs nor radial striations present on type material; ears of right valve about equal in length, smooth, with occasional subdued growth lines; byssal notch under right anterior ear slightly developed; hinge apparently similar or identical to that of *Pecten coalingaensis*. Dimensions of type: Height, 2¼ inches (54 mm.); width, 2¼ inches (57 mm.) ventricosity of right valve, 15/16 inch (24 mm.); length of hinge, 13/32 inch (27 mm.)

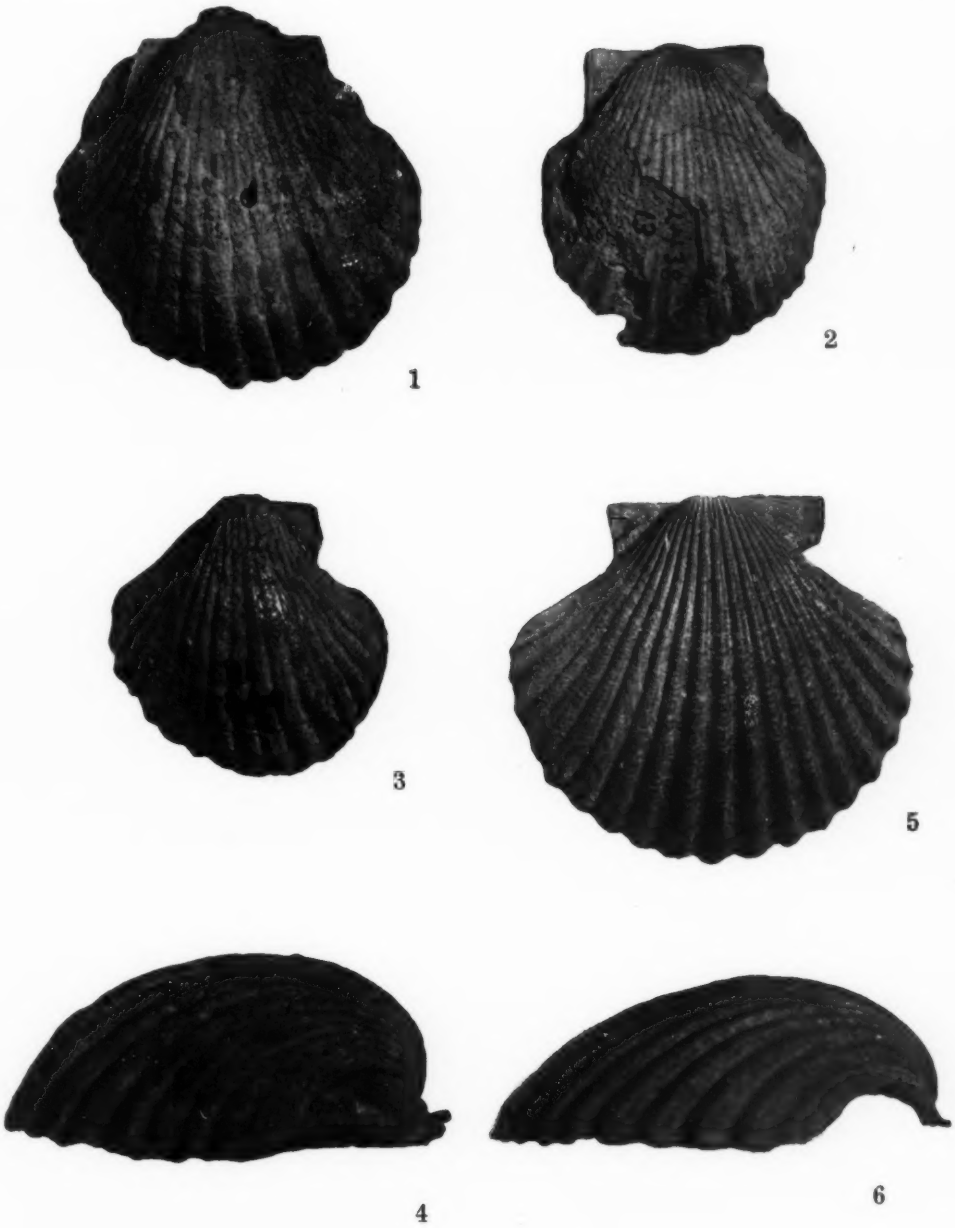
Holotype.—Catalogue No. 10441 in the collection at the University of California at Los Angeles; a large right valve adherent to an echinoid, from UCLA Locality 435, sandstone fossil reef on east side of valley of San Juan Creek, at elevation of about 1500 feet above sea level, in west middle half of section 32, Township 28 south, Range 16 East (Mount Diablo Base and Meridian), eastern San Luis Obispo County, California. Stratigraphic position: approximately at conformable contact between lower and upper Neroly, in lower half of the upper third of the Miocene. U. S. Grant and E. H. Quayle, collectors, July 1933. Associated fauna: *Lyropecten estrellanus*, *Astrodapsis* sp. (at Locality 437, same horizon NW across valley) and *Ostra panzana* Conrad, etc.

Paratype.—California Academy of Sciences, No. 7729, from UCLA Locality 438,

EXPLANATION OF PLATE 124

FIGS. *1–4*—*Pecten* (*Pecten*) *juanensis*, new species, Grant and Stevenson, from the Upper Miocene of eastern San Luis Obispo County, California. All figures approximately natural size. *1*, right valve of Holotype. Note the smooth ears. *2*, right valve of Paratype, California Academy of Sciences Collection. *3*, right valve of Paratype in U. S. National Museum. *4*, side view of the Holotype of *Pecten juanensis*, showing the ventricosity of the right valve.

5, *6*—*5*, *Pecten coalingaensis* Arnold, from Pliocene of Kettleman Hills, California. Right valve of hypotype, catalogue number 3445, Univ. of Calif. at Los Angeles, for comparison; *6*, side view of right valve of *P. coalingaensis* for comparison of ventricosity with that of *P. juanensis* shown in fig. *4*.



Grant and Stevenson, Upper Miocene *Pecten*

in the same fossil reef about 3.6 miles North 29° West of UCLA Locality 435, sandstone, strike N29W, 85° northeasterly.

Paratype.—U. S. National Museum, from UCLA Locality 435.

This new species differs from *Pecten coalingaensis* Arnold of the upper Pliocene in its lack of ribs on the ears of the right valve, in its lower, broader, less convex ribs with narrower interspaces, and in its greater ventricosity. Both species appear to have the same average number of ribs, which is about 20 on the right valve.

From *Pecten vogdesi* Arnold, the new Miocene species differs in its smaller size, less ventricosity and smooth ears. *P. vogdesi* has 3 or 4 strong ribs on the right anterior ear with more, slightly less prominent ribs on the posterior ear. Both ears of the new Miocene species are smooth.

The similarities between the new species and *P. coalingaensis* Arnold (Arnold in Anderson 1905, p. 197; Arnold 1906, p. 97) is greater than the similarities between the new species and *Pecten bellus* Conrad (Proc. A. N. Sci. Phila. 1856, p. 312; Arnold 1906, p. 95). We believe that *P. juanensis*, *P. coalingaensis* and *P. vogdesi* are genetically related and form a clan to which *P. bellus* is only related as a possible off-shoot from the upper Miocene species here described, or from an earlier common ancestor. The matrix of the surrounding sediment and the associated fauna indicate that *P. juanensis* probably was a dweller in shallow, warm water of normal salinity. The chief interest in this new upper Miocene species is that it appears to be ancestral to *P. coalingaensis* and *P. vogdesi*.

Types of this new species were examined by Dr. Leo G. Hertlein of the California Academy of Sciences, an authority on Pectens, who concurs with us in its distinctness from the other species mentioned above. Dr. Hertlein called our attention to the apical angle of the umbones, which in the new species is about 90 degrees, but in *P. vogdesi* is about 95 to 100 degrees. He also mentioned that *Pecten heimi* Hertlein (Proc. Calif. Acad. Sci. 1925, pp. 9–10) of the lower Pliocene(?) of Lower California, Mexico has but weakly sculptured ears. In general appearances it closely resembles the new Miocene species which, however, has unsculptured ears. Possibly the relationship of the new species is closer to *P. heimi* than to *P. vogdesi*.

REFERENCES

ARNOLD, RALPH, 1905, in F. M. Anderson, Proc. Calif. Acad. Sci., Ser. 3, Vol. 2, p. 197, pl. 18 figs. 94–98.

——, 1906, U. S. Geol. Surv. Prof. Paper 47, p. 97, pl. 4, figs. 4, 4a, 5.

Proc. Acad. Nat. Sci. Phila. for 1856, p. 312, (1857)

Proc. Calif. Acad. Sci., Ser. 4, Vol. 14, No. 1, pp. 9–10, pl. 1, fig. 3, pl. 3, fig. 3, July 1925.

JOURNAL OF PALEONTOLOGY, VOL. 22, NO. 6, P. 806, NOVEMBER 1948

ERRATA

For: C. M. Bramine Caudri, Note on the Stratigraphic Distribution of Lepidorbitoides, Journal of Paleontology, Vol. 22, no. 4, pp. 473–481, pls. 73, 74, July 1948.

p. 473 left hand column line 6 from bottom: should be Danian

p. 474 right hand column line 7 from top: 5) should be cancelled

right hand column line 3 from bottom: in a satisfactory way, *but* because

p. 476 explanation of plate:

for fig. 2: Valle Hondo formation

for fig. 4: Barbados

opposite p. 477: on plate 74 interchange the numbers of figures 3 and 7

p. 479 under III. Venezuela: limestone of San Juan designation of the age of the Valle Hondo Formation (line 18 from bottom) should be: *Paleocene or Lower Eocene*

p. 481

bibliography of Silvestri: n*uo*vo giacimento

bibliography of Sutton: add: fig. 1–11, 1 map.

JOURNAL OF PALEONTOLOGY

INDEX TO VOLUME 22

AUTHOR INDEX

		No.	Page
1.	BARTRUM, J. A., Two undetermined New Zealand Tertiary fossils	4	488
2.	BELL, W. CHARLES, Acetic acid etching applied to Cambrian brachiopods	1	101
3.	BOUSKA, JOSEF, Holynocrinus, new crinoid genus from the Middle Devonian of Bohemia	4	520
4.	BRANSON, E. B. and MEHL, M. G., Conodont homonyms and names to replace them	4	527
5.	BROWN, IDA A., Ordovician brachiopods from Junee District, Tasmania	1	35
6.	BURMA, BENJAMIN H., Studies in quantitative paleontology: I. Some aspects of the theory and practice of quantitative invertebrate paleontology	6	725
7.	BURSCH, J. G., Über morphogenetische untersuchungen an Grossforaminiferen, by Otto Renz and H. Küpper (Review of)	4	533
8.	CASTER, KENNETH E., Anelideos poliquetos dos folhelos devonianos do Paraná, by Frederico Waldemar Lange (Review of)	5	647
9.	CAUDRI, C. M. BRAMINE, Note on the stratigraphic distribution of *Lepidorbitoides* (See also Errata, p. 806)	4	473
10.	CLARK, T. H., *Theodenisia*, new name replacing *Denisia* Clark	5	643
	COLBERT EDWIN H., see NEWELL, NORMAN D. (50)		
11.	COLOM, G., Fossil tintinnids: loricated Infusoria of the order of Oligotricha	2	233
12.	COOKE, C. WYTHE, *Arbia* and *Dixieus*, two new genera of echinoids	5	606
13.	COOKE, C. WYTHE, Eocene echinoids from Panama	1	91
14.	TEN DAM, A., *Cribroparella*, a new genus of Foraminifera from the Upper Miocene of Algeria	4	486
15.	TEN DAM, A., Foraminifera from the Middle Neocomian of the Netherlands	2	175
16.	DAVID, LORE R., Halosauridae from the California Tertiary	2	94
17.	DECKER, CHARLES E., A new species of hydrozoan from the Athens shale of Virginia	4	528
18.	DORREEN, J. M., A Foraminifera fauna from the Kaiatan stage (upper Eocene), of New Zealand	3	281
	DOWNS, R. H., see MILLER, A. K. (46)		
19.	DURHAM, J. WYATT, and ROBERTS, WAYNE A., Cretaceous asteroids from California	4	432
20.	EGUCHI, MOTOKI, A new *Spongiomorpha* from the *Orbitolina* sandstone of Iwate prefecture in Japan	3	365
21.	EGUCHI, MOTOKI, Fossil Helioporidae from Japan and the South Sea Islands	3	362
	FERRIS, BERNARD J., see JOHNSON, J. HARLAN (38)		
22.	FREDERICKSON, E. A., Upper Cambrian trilobites from Oklahoma	6	798
23.	FRITZ, MADELEINE A., Cambrian Bryozoa more precisely dated	3	373
24.	FRIZZELL, DON L., Lectotype of *Spirolectammina grzybowskii*	1	106
25.	FRIZZELL, DON L., Orthography and type designations of *Dictyoconus* Blanckenhorn (Foraminifera)	3	370
26.	GRANT, U. S., and STEVENSON, ROBERT E., A new *Pecten* from the Upper Miocene of California	6	804
27.	GRICE, CHARLES R., *Manorella*, a new genus of Foraminifera from the Austin chalk of Texas	2	222
28.	GRIMSDALE, T. F., Occurrence of *Lepidocyclina pustulosa* (H. Douvillé) in Morocco	4	529
29.	GUNTER, GIRDON, Erratum for "Extended remarks on relationships of marine animals to salinity"	3	388
30.	HAAS, OTTO, Implications of *Prionotropis* Meek being a homonym	1	106
31.	HAAS, OTTO, Legal status of opinions rendered by the I.C.Z.N.	5	641
32.	HAAS, OTTO, *Madrasites* a synonym of *Kossmaticeras* s.str.	5	642
33.	HAAS, OTTO, Monophyletic or polyphyletic derivation of ammonites?	1	104
34.	HATAI, KOTORA, New Tertiary Brachiopoda from Japan	4	494
	HEEZEN, BRUCE C., see YOUNGQUIST, WALTER (94)		
	HIBBARD, RAYMOND R., see YOUNGQUIST, WALTER (95)		
35.	HOFKER, J., On *Asterigerina gurichi* (Franke), and remarks on polymorphism and the stratigraphic use of Foraminifera	4	509
36.	HOUGH, JEAN RINGIER, A systematic revision of *Daphoenus* and some allied genera	5	573
	HOWELL, B. F., see JOHNSON, J. HARLAN (39)		
37.	JEFFORDS, RUSSELL M., New Pennsylvanian dibunophyllid corals	5	617

38. JOHNSON, J. HARLAN, and FERRIS, BERNARD J., Eocene Algae from Florida 6 762
39. JOHNSON, J. HARLAN, and HOWELL, B. F., a new Cretaceous alga from Kansas 5 632
40. KJELLESVIG-WAERING, ERIK N., Two new eurypterids from the Silurian of Indiana .. 4 465
41. KNIGHT, J. BROOKES, Report of Policy Board of Joint Committee on Zoological Nomenclature on Paleontology in America for 1947 ..... 5 643
42. KNIGHT, J. BROOKES, and WELLER, J. MARVIN, The application of opinion 138 to some recently published names 1 107
43. LALICKER, CECIL G., A new genus of Foraminifera from the Upper Cretaceous 5 624
44. LEROY, L. W., The foraminifer *Orbulina universa* d'Orbigny, a suggested Middle Tertiary time indicator 4 500
45. LOCHMAN, CHRISTINA, New Cambrian trilobite genera from northwest Sonora, Mexico 4 451
MEHL, M. G., see BRANSON, E. B. (4)
46. MILLER, A. K., and DOWNS, R. H., A cephalopod fauna from the type section of the Pennsylvanian "Winslow formation" of Arkansas 6 672
47. MILLER, A. K., and PARIZEK, ELDON J., A Lower Permian ammonoid fauna from New Mexico 3 350
48. MILLER, A. K., and YOUNGQUIST, WALTER, The cephalopod fauna of the Mississippian Barnett formation of Central Texas 6 649
MILLER, A. K., see STURGEON, MYRON T. (75), YOUNGQUIST, WALTER (96)
49. NEWELL, NORMAN D., Infraspecific categories in invertebrate paleontology 2 225
50. NEWELL, NORMAN D., and COLBERT, EDWIN H., Paleontologist—Biologist or Geologist? 2 264
51. NISIYAMA, SYOZO, *Astrodapsis* in Japan 5 601
52. OKULITCH, VLADIMIR J., Lower Cambrian Pleospongia from the Purcell Range of British Columbia, Canada 3 340
ORIEL, STEVEN S., see SWARTZ, FRANK M. (76)
53. PALMER, KATHERINE VAN WINKLE, DOROTHY K. PALMER, 1897–1947 ..... 4 518
PARIZEK, ELDON J., see MILLER, A. K. (47)
54. PECK, RAYMOND E., A Triassic crinoid from Mexico 1 81
55. PECK, RAYMOND E., and REKER, CARL E., Eocene Charophyta from North America . 1 85
56. POULSEN, CH., *Grinnellaspis*, new name, replacing *Actinopeltis* Poulsen, 1946 ..... 1 107
57. RASETTI, FRANCO, Cephalic sutures in *Loganopeltis* and the origin of "hypoparian" trilobites 1 25
58. RASETTI, FRANCO, Lower Cambrian trilobites from the conglomerates of Quebec (exclusive of the Ptychopariidea) 1 1
59. RASETTI, FRANCO, Middle Cambrian trilobites from the conglomerates of Quebec (exclusive of the Ptychopariidea) 3 315
60. RAU, WELDON W., Foraminifera from the Miocene Astoria formation in southwestern Washington 6 774
61. RAU, WELDON W., Foraminifera from the Porter shale (Lincoln formation), Grays Harbor County, Washington 2 152
REIMANN, IRVING G., see YOUNGQUIST, WALTER (95)
REKER, CARL C., see PECK, RAYMOND E. (55)
62. RICHARDSON, EUGENE S., JR., Paleogeography and nomenclature 3 369
ROBERTS, WAYNE A., see DURHAM, J. WYATT (19)
63. RUSSELL, LORIS S., The dentary of *Troodon*, a genus of theropod dinosaurs 5 625
64. SCHMIDT, RUTH A. M., Magnetic separation of microfossils 4 530
65. SCHMIDT, RUTH A. M., Ostracoda from the Upper Cretaceous and Lower Eocene of Maryland, Delaware, and Virginia 4 389
66. SCHOPF, JAMES M., Pteridosperm male fructifications: American species of *Dolerotheca*, with notes regarding certain allied forms 6 681
67. SINCLAIR, G. WINSTON, Three notes on Ordovician cystids 3 301
68. SOHN, I. G., Two new marine ostracodes from the Tertiary of Washington 4 482
69. STAINFORTH, R. M., Applied micropaleontology in coastal Ecuador 2 113
70. STEPHENSON, L. W., *Cypraea corsicanana*, new name for *C. gracilis* Stephenson, preoccupied 5 642
STEVENSON, ROBERT E., see GRANT, U. S. (26)
71. STOYANOW, ALEXANDER, Molluscan faunule from Devonian Island Mesa beds, Arizona 6 783
72. STRIMPLE, HARRELL L., Notes on *Phanocrinus* from the Fayetteville formation of northeastern Oklahoma 4 490
73. STUMM, ERWIN C., A revision of some Mississippian tetracoral genera 1 68
74. STUMM, ERWIN C., Upper Devonian compound tetracorals from the Martin limestone. 1 40
75. STURGEON, MYRON T., and MILLER, A. K., Some additional cephalopods from the Pennsylvanian of Ohio 1 75
76. SWARTZ, FRANK M., and ORIEL, STEVEN S., Ostracoda from the Middle Devonian Windom beds in western New York 5 541
77. SYLVESTER-BRADLEY, P. C., The ostracode genus *Cythereis* 6 792

78. TEICHERT, CURT, Middle Devonian goniatites from the Buchan District, Victoria 1 60
79. TEICHERT, CURT, A simple device for coating fossils with ammonium chloride 1 102
80. THALMANN, HANS E., Bibliography and Index to new genera, species, and varieties of Foraminifera for the year 1946 ..... 2 193
81. TURNBULL, WILLIAM D., Cocoa sand type locality 3 372
82. VOORTHUYSEN, J. H. VAN, Upper Cretaceous Foraminifera of minute size in the marine Pleistocene (Icenian) sands of the Netherlands 4 525
83. WARREN, P. S., Chimaerid fossil egg capsules from Alberta 5 630
84. WARTHIN, A. SCOTT, Ostracode genotypes designated by S. A. Miller 5 645
85. WELLER, J. MARVIN, Paleontologist—Biologist and Geologist 2 268
86. WELLER, J. MARVIN, Principles of micropaleontology, by Martin F. Glaessner (Review of) 5 608
WELLER, J. MARVIN, see KNIGHT, J. BROOKES (42) 2 270
87. WELLS, JOHN W., Lower Cretaceous corals from Trinidad, B.W.I. 5 608
88. WHITTINGTON, H. B., A new Lower Ordovician trilobite 5 567
89. WILSON, JAMES L., Two Upper Cambrian *Elvinia* zone trilobite genera 1 30
90. WILSON, JOHN ANDREW, Cope's types of fossil fishes in the collection of the Bureau of Economic Geology, the University of Texas 3 368
91. WILSON, JOHN ANDREW, A small amphibian from the Triassic of Howard County, Texas 3 359
92. WOOD, ALAN, Sectioning small Foraminifera 4 530
93. YEN, TENG-CHIEN, Eocene fresh-water Mollusca from Wyoming 5 634
94. YOUNGQUIST, WALTER, and HEEZEN, BRUCE C., Some Pennsylvanian conodonts from Iowa 6 767
95. YOUNGQUIST, WALTER, HIBBARD, RAYMOND R., and REIMANN, IRVING G., Additions to the Devonian conodont faunas of western New York 1 48
96. YOUNGQUIST, WALTER, and MILLER, A. K., Additional conodonts from the Sweetland Creek shale of Iowa 4 440
YOUNGQUIST, WALTER, see MILLER, A. K. (48)

SUBJECT INDEX

Acetic acid etching applied to Cambrian brachiopods (2).
Actinopeltis Poulsen, replaced by *Grinnellaspis* (56).
Africa: Occurrence of *Lepidocyclina pustulosa* in Morocco (28); Upper Miocene Foraminifera (14).
Alabama: Oligocene echinoids (12).
Alberta: Cretaceous chimaerid egg capsules (83); Upper Cretaceous dinosaur *Troodon* (63).
Algeria: Foraminifera, Upper Miocene (14).
Ammonites, Monophyletic or polyphyletic origin (33).
Ammonium chloride, simple device for coating fossils (79).
Ammonoids, Permian, Lower, New Mexico (47).
Amphibian, small, from Texas Triassic (91).
Arbia: Oligocene echinoids (12).
Arkansas: Cephalopod fauna from Pennsylvanian "Winslow formation" type section (46); Foraminifera, Upper Cretaceous (43).
Asterigerina gurichi (Franke) (35).
Asteroids, Cretaceous, California (19).
Astoria formation Foraminifera, southwestern Washington (60).
Astrodapsis in Japan (51).
Athens shale, Hydrozoa, Virginia (17).
Arizona: Devonian Mollusca (71); Martin limestone compound tetracorals (74).
Austin chalk, *Manorella* (Foraminifera), Texas (27).
Australia: Middle Devonian goniatites, Buchan District, Victoria (78).
Balearic Islands: Fossil tintinnids (11).
Barnett formation, Cephalopoda, central Texas (48).
Bibliography and index, Foraminifera (80).
Biglobigerinella, Arkansas Upper Cretaceous Foraminifera (43).
Biologist and geologist (85).
Biologist or geologist (50).
Bohemia: Middle Devonian *Holynocrinus* (3).
Brachiopoda: Cambrian etched with acetic acid (2); Ordovician, Lower, Tasmania (5); Tertiary, Japan (34).
British Columbia: Lower Cambrian Pleospongia (52).
Bryozoa: Cambrian, more precisely dated (23).
Calcareous algae: Kansas Cretaceous (39).
California: Cretaceous asteroids (19); Miocene, Upper, *Pecten* (26); Tertiary *Halosauridae* (16).
Calpionellae, Fossil infusoria (11).
Cambrian: Brachiopods etched with acetic acid (2); Bryozoa more precisely dated (23); Cambrian

Lower: British Columbia Plespongia (52); Trilobita, Quebec (58); Cambrian, Middle: Trilobita, Quebec; Cambrian, Upper: *Elvinia* zone trilobita (89); *Loganopeltoides* (57); Trilobita, Oklahoma (22).
Canada: Cambrian Bryozoa (23); Lower Cambrian Pleospongia (52).
Caribbean: *Lepidorbitoides*, Distribution of (9).
Cephalopoda: Ammonoids, New Mexico Lower Permian (47); Australia Middle Devonian (78); Implications of *Prionotropis* being a synonym (30); *Madrasites* a synonym of *Kossmaticeras* s.str. (32); Mississippian Barnett formation of central Texas (48); Pennsylvanian of Ohio (75); Pennsylvanian "Winslow formation" of Arkansas (46).
Charophyta: Eocene, North America (55).
Chimaerid egg capsules: Cretaceous of Alberta (83).
Cocoa sand type locality (81).
Colombia: Guaduas formation (9).
Conodonts: Additional, from Sweetland Creek shale (Upper Devonian) Iowa (96); Homonyms (4); Iowa Pennsylvanian (94); Western New York Devonian (95).
Cope's types of fossil fishes (90).
Corals: Dibunophyllid, Pennsylvanian of Oklahoma and Kansas (37); Helioporidae, Lower Cretaceous of Japan and South Sea Islands (21); Lower Cretaceous, Japan (20); Lower Cretaceous, Trinidad, B.W.I. (87); Mississippian, revision of some tetracoral genera (73).
Cretaceous: Asteroids, California (19); Calcareous algae, Kansas (39); Chimaerid egg capsules, Alberta (83); Foraminifera (24); Foraminifera, Austin chalk (27); *Lepidorbitoides*, distribution of (9); Lower Cretaceous corals, Japan (20); Trinidad (87); Lower Cretaceous Helioporidae (21); Neocomian Foraminifera, Netherlands (15); Ostracoda (77); Tintinnids (11); Upper Cretaceous: *Biglobigerinella* (43); Troodon (63); Foraminifera in Pleistocene sands (82); Ostracoda (55).
Cribroparella, Upper Miocene Foraminifera, Algeria (14).
Crinoidea: *Holynocrinus*, Middle Devonian, Bohemia (3); *Phanocrinus*, Fayetteville formation, Oklahoma (72); Triassic, Mexico (54).
Cypraea corsicanana Stephenson, new name for *C. gracilis* (70).
Cystoids: Ordovician (67).
Cythereis, the ostracode genus (77).
Daphoenus and some allied genera, Systematic revision of (36).
Delaware: Ostracoda from Upper Cretaceous and Lower Eocene (65).
Dentary of *Troodon* (63).
Devonian: Conodonts, western New York (95); Mollusca, Arizona (71).
Devonian, Middle: Holynocrinus, Bohemia (3); New York Ostracoda (76); Victoria goniatites (78).
Devonian, Upper; Additional Sweetland Creek shale conodonts (96); Compound tetracorals (74).
Dibunophyllid corals, Pennsylvanian, Kansas and Oklahoma (37).
Dictyoconus Blanckenhorn (25).
Dinosaurs: Theropod, dentary of *Troodon* (63).
Distribution, stratigraphic, of *Lepidorbitoides* (9).
Dixieus, Eocene echinoids (12).
Dolerotheca, American species of (66).
Echinodermata: Asteroids, California Cretaceous (19).
Echinoidea: *Astrodapsis* in Japan (51); Eocene, Panama (13); Tertiary, Alabama, Florida (12).
Ecology: Relationships of marine animals to salinity, erratum for extended remarks on, (29).
Ecuador: Applied micropaleontology in coastal, (69).
Elvinia zone trilobites, Mid-continent Upper Cambrian (89).
Eocene: Algae, Florida (38); Cocoa sand type locality (81); Echinoids (12); Fresh-water Mollusca (93); *Lepidocyclina pustulosa* (28); New Zealand Foraminifera (18); North American Charophyta (55); Ostracoda, Lower Eocene (65).
Etching with acetic acid (2).
Europe: Middle Devonian *Holynocrinus* from Bohemia (3).
Eurypterids: Silurian, Indiana (40).
Evolution of ammonites (33).
Extended remarks on relationships of marine animals to salinity, erratum for (29).
Fayetteville formation: *Phanocrinus*, Oklahoma (72).
Fishes: Chimaerid egg capsules (83); Copes types of (90).
Florida: Eocene algae (38); Eocene echinoids (12).
Foraminifera: *Asterigerina gurichi*, polymorphism and stratigraphic use of (35); Bibliography and index, 1946 (80); Cretaceous, Upper, of Arkansas (43); Cretaceous, Upper, in Pleistocene sands (82); *Dictyoconus* Blanckenhorn, orthography and type designations (25); Eocene, Upper, New Zealand (18); Lepidocyclina pustulosa, Morocco (28); *Manorella* from Austin chalk, Texas (27); Miocene, Washington (60); Miocene, Upper, Algeria (14); Neocomian, Upper, Netherlands (15); *Orbulina universa* as Middle tertiary time indicator (44); Sectioning of small (92); *Spiroplectammina grzybowskii* (24); Stratigraphic distribution of *Lepidorbitoides* (9); Tertiary, coastal Ecuador (69); Tertiary, Early, of Washington (61).
Fossils: New Zealand Tertiary (1).

Fresh-water Mollusca, Wyoming Eocene (93).
Fructifications of *Dolerotheca* (66).
Genotypes: Of ostracodes, designated by S. A. Miller (84).
Goniatites: Middle Devonian of Australia (78).
Grays Harbor County, Washington, Foraminifera (61).
Halosauridae: California Tertiary (16).
Helioporidae: Fossil, Japan and South Sea Islands (21).
Holynocrinus: Middle Devonian, Bohemia (3).
Homonym, implication of, in *Prionotropis* (30).
Homonyms: Conodont (4).
Howard County, Texas: Triassic amphibian (91).
Hydrozoa: Lower Ordovician, Virginia (17).
Icenian (Pleistocene) with Upper Cretaceous Foraminifera (82).
Illinois: Pennsylvanian plants, Dolerotheca (66).
Index to new genera, species and varieties of Foraminifera for the year 1946 (80).
Indiana: Silurian eurypterids (40).
Infraspecific categories in invertebrate paleontology (49).
Infusoria: Fossil tintinnids (11).
International Commission on Zoological Nomenclature, Legal status of opinions (31).
Invertebrate paleontology, Infraspecific categories in, (49).
Iowa: Additional Sweetland Creek conodonts (96); Pennsylvanian conodonts (94).
Island Mesa beds, Devonian, Mollusca of, (71).
Japan: *Astrodapsis* (51); Fossil Helioporidae (21); Lower Cretaceous corals (20); New Tertiary Brachiopoda (34).
Junee District, Tasmania, Lower Ordovician Brachiopoda (5).
Jurassic: Ostracoda (77); Tintinnids (11).
Kaiatan stage (Upper Eocene), Foraminifera, New Zealand (18).
Kansas: Cretaceous calcareous algae (39); Pennsylvanian corals (37).
Kossmaticeras, s.str. and *Madrasites* (32).
Legal status of opinions rendered by the International Commission on Zoological Nomenclature (31).
Lepidocyclina pustulosa, occurrence in Morocco (28).
Lepidorbitoides, stratigraphic distribution (9).
Lincoln formation: Tertiary Foraminifera (61).
Loganopeltoides, cephalic sutures and origin of hypoparian trilobites (57).
Madrasites synonym of Kossmaticeras s.str. (32).
Magnetic separation of microfossils (64).
Manorella, Foraminifera, Austin chalk, Texas (27).
Martin limestone, Upper Devonian tetracorals (74).
Maryland: Ostracoda, Upper Cretaceous, Lower Eocene (65).
Mexico: New Cambrian trilobite genera (45), Triassic Crinoidea (54).
Microfossils, magnetic separation of (64).
Micropaleontology, applied, in coastal Ecuador (69).
Miocene: *Daphoenus*, revision and related genera (36); Foraminifera (60).
Miocene, Upper: Foraminifera (14); *Pecten* (26).
Mississippian: Barnett formation cephalopods (48); Fayetteville *Phanocrinus* (72); Tetracoral genera (73).
Mollusca: Devonian, Arizona (71); Eocene, Wyoming fresh water (93).
Monophyletic or polyphyletic derivation of ammonites? (33).
Morocco: Occurrence of *Lepidocyclina pustulosa* (28).
Neocomian: Infusoria (tintinnids) (11); Foraminifera, Netherlands (15).
Neogene: *Astrodapsis* in Japan (51).
Netherlands: *Asterigerina gruichi* (35); Middle Neocomian Foraminifera (15); Pleistocene Icenian sands with Upper Cretaceous Foraminifera (82).
Nevada: Lower Ordovician trilobites (88).
New genera of trilobites, Cambrian, Mexico (45).
New Mexico: Lower Permian ammonoids (47).
New names: Conodont (4); *Cypraea corsicanana* for *C. gracilis* Stephenson (70); *Grinnellaspis* for *Actinopeltis* Poulsen (56).
New York: Conodonts (95); Ostracoda (76).
New Zealand: Eocene Foraminifera (18); Tertiary fossils (1).
Nomenclature: and paleogeography (62); Zoological, application of opinion 138 to some recently published names, (42).
North America: Eocene Charophyta (55).
Ohio: Pennsylvanian Cephalopoda (75).
Oklahoma: Cambrian trilobites (22); Pennsylvanian corals (37); *Phanocrinus* (72).
Oligocene: Echinoides (12).
Oligotricha: Fossil Infusoria (11).
Ontario: Ordovician cystids (67).

Opinion 138, application of (42).
Orbitolina sandstone (20).
Orbulina universa (44).
Ordovician: Brachiopoda (5); Cystids (67); Hydrozoan (17); Trilobita (88).
Orthography and type designations of *Dictyoconus* (25).
Ostracoda: Cretaceous and Eocene (65); *Cythereis* (77); Devonian (76); Genotypes (84); Tertiary (68).
Paleogeography and nomenclature (62).
Paleontologist: Biologist and geologist (85); Biologist or geologist? (50).
Paleontology: Infraspecific categories in invertebrate (49); Quantitative, invertebrate (6).
Palmer, Dorothy K. (53).
Panama: Eocene echinoids (13).
Pecten, Upper Miocene, California (26).
Pelecypoda: Upper Miocene *Pecten*, California (26).
Pennsylvanian: Cephalopoda Arkansas (46); Ohio (75); Conodonts, Iowa (94); Corals, Oklahoma and Kansas (37); *Dolerotheca* (66); "Winslow formation," fauna (46).
Permian, Lower: New Mexico ammonoids (47).
Phanocrinus, Mississippian, Oklahoma (72).
Plants: *Dolerotheca* (66); Eocene Charophyta (55).
Pleistocene, marine, with Upper Cretaceous Foraminifera (82).
Pleospongia: Lower Cambrian, British Columbia (52).
Polymorphism, Foraminifera (36).
Porter shale Foraminifera (61).
Prionotropis Meek, Implications of being a homonym (30).
Pteridosperms: *Dolerotheca* (66).
Purcell Range, British Columbia: Lower Cambrian Pleospongia (52).
Quebec: Cystids, Ordovician (67); *Loganopeltoides*, Upper Cambrian (57); Trilobites, Lower Cambrian (58); Trilobites, Middle Cambrian (59).
Quantitative paleontology, Invertebrate (6).
Recent: Ostracoda (77).
Report of Policy Board of Joint Committee on Zoological Nomenclature on Paleontology in America (41).
Reviews: Anelidos polyquetos folhelos devonianos do Paraná, by Frederico Waldemar Lange (8); Principles of micropaleontology, by Martin F. Glaessner (86); Über morphogeneticsche untersuchungen an Grossforaminiferen, by Otto Renz and H. Küpper (7).
Revision of some Mississippian tetracoral genera (73).
Sectioning small Foraminifera (92).
Separation, magnetic, of microfossils (64).
Significance of *Spongiomorpha*, Lower Cretaceous of Japan (20).
Silurian: Eurypterids, Indiana (40).
Society Records and Activities: *Paleontological Society*, Membership list, p. 375, nominations for officers for 1949, p. 387; *Society of Economic Paleontologists and Mineralogists*, Membership list, p. 272, Reports and minutes, 22nd annual meeting, p. 534.
Sonora, Mexico: New Cambrian trilobite genera (45).
South Dakota: Upper Cambrian trilobites (89).
South Sea Islands: Fossil Helioporidae (21).
Spiroplectammina grzybowskii, Lectotype of (24).
Spongiomorpha, Lower Cretaceous Corals, Japan (20).
Statistical method in paleontology (6).
Statistical study of *Asterigerina gurichi* (35).
Stratigraphic use of Foraminifera, Remarks on, (35).
Studies, quantitative paleontology (6).
Sweetland Creek shale, Additional conodonts from, (96).
Tasmania: Lower Ordovician brachiopods (5).
Techniques: Acetic acid etching (2); Ammonium chloride device (79); Magnetic separation of microfossils (64); Sectioning small Foraminifera (92).
Tertiary: *Astrodapsis* in Japan (51); Brachiopoda, Japan (34); Foraminifera, Washington (61); Fossils, New Zealand (1); Halosauridae, California (16); *Lepidorbitoides* (9); Micropaleontology, coastal Ecuador (69); *Orbulina universa* (44); Ostracoda (77); Ostrcaoda, marine (68).
Tetracorals: Compound, Arizona (74); Mississippian, Revision of genera (73).
Texas: Amphibian (91); Cephalopod fauna (48); Foraminifera (*Manorella*) (27); Trilobites, Upper Cambrian (89).
Theodenisia, new name for *Denisia* Clark (10).
Theory and practice of quantitative invertebrate paleontology (6).
Tintinnids: fossil (11).
Tithonian: Infusoria (tintinnids) (11).
Triassic: Amphibian (91); Crinoidea (54).

Trilobites: Cambrian, Mexico (45); Cambrian (Lower) Quebec (58); Cambrian (Middle) Quebec (59); Cambrian (Upper) *Elvinia* zone (89); Cambrian (Upper) Oklahoma (22); *Denisia* Clark replaced by *Theodenisia* Clark (10); *Actinopeltis* Poulsen replaced by *Grinnellaspis* Poulsen (56); Ordovician (Lower) new genus (88); Origin of "hypoparian" (57).
Trinidad: *Lepidorbitoides* (9); Lower Cretaceous (87).
Troodon, dentary of (62).
Type locality, of Cocoa sand (81).
Types of fossil fishes, Copes (90).
Venezuela: *Lepidorbitoides* (9).
Vertebrates: Amphibia (91); Chimaerid egg capsules (83); Copes types of fossil fishes (90); *Daphoenus* and allied genera (36); Halosauridae (16); *Troodon*, Dentary of (63).
Victoria: Middle Devonian (78).
Virginia: Hydrozoa (17); Ostracoda, Upper Cretaceous, Lower Eocene (65).
Washington: Foraminifera, Early Tertiary (61); Foraminifera, Miocene (60); Ostracoda, Tertiary (68)
West Indies: Lower Cretaceous corals (87).
Windom (Middle Devonian) Ostracoda (76).
"Winslow formation" (Pennsylvanian) Cephalopoda (46).
Wyoming: Cambrian trilobites (89); Eocene Mollusca (93).
Zoological Nomenclature, Report of Policy Board (41).

OFFICERS OF THE SOCIETIES

THE SOCIETY OF ECONOMIC PALEONTOLOGISTS AND MINERALOGISTS

For the year ending March 1949

President, R. Dana Russell, San Diego, Calif.

First Past-President, James A. Waters, Dallas, Tex.

Second Past-President, F. W. Rolshausen, Houston, Tex.

Vice-President, J. B. Garrett, Jr., Houston, Tex.

Secretary-Treasurer, H. B. Stenzel, Austin, Tex.

Editors

J. Marvin Weller, Chicago, Ill., for paleontology.

W. H. Twenhofel, Orlando, Fla., for mineralogy.

THE AMERICAN ASSOCIATION OF PETROLEUM GEOLOGISTS

For the year ending March 1949

President, Paul Weaver, Houston, Tex.

Past-President, C. E. Dobbin, Denver, Colo.

Vice-President, Roy M. Barnes, Los Angeles, Calif.

Secretary-Treasurer, J. V. Howell, Tulsa, Okla.

Editor, C. L. Moody, Shreveport, La.

THE PALEONTOLOGICAL SOCIETY

For the year ending December 1948

President, Wendell Woodring, Washington, D.C.

Vice-President, C. Wythe Cooke, Washington, D.C.

Secretary, H. E. Vokes, Baltimore, Md.

Treasurer, Frank M. Swartz, State College, Pa.

Editor, A. Scott Warthin, Poughkeepsie, N.Y.

Chairman, Pacific Coast Section, J. Wyatt Durham, Berkeley, Calif.

Ex-Presidents

Chester Stock, Pasadena, Calif., 1945.
J. Brookes Knight, Washington, D. C., 1946.
R. C. Moore, Lawrence, Kans., 1947.

JOINT COMMITTEE ON ZOOLOGICAL NOMENCLATURE FOR PALEONTOLOGY IN AMERICA

Sponsored by the Society of Economic Paleontologists and Mineralogists, The Paleontological Society, and the Society of Vertebrate Paleontology in support of the International Commission on Zoological Nomenclature.

Policy Board

Raymond C. Moore, *Chairman* (SEPM), J. B. Reeside, Jr., (PS); A. S. Romer (SVP)

Members

John B. Reeside, Jr. G. Arthur Cooper Norman D. Newell George Gaylord Simpson	1946–1948
Alfred S. Romer Donald L. Frizzell A. Myra Kern Katherine V. W. Palmer	1947–1949
J. Brookes Knight Raymond C. Moore G. Winston Sinclair John W. Wells	1948–1950

Address all communications to the chairman, Raymond C. Moore, University of Kansas, Lawrence, Kansas.

THE GEOLOGICAL SOCIETY OF AMERICA

For the year ending December 1948

President, James Gilluly, Los Angeles, Calif.
Past-President, A. I. Levorsen, Stanford University, Calif.

Vice-Presidents

Chester R. Longwell, New Haven, Conn.
Kirk Bryan, Cambridge, Mass.
Raymond C. Moore, Lawrence, Kans.
Martin J. Buerger, Cambridge, Mass.

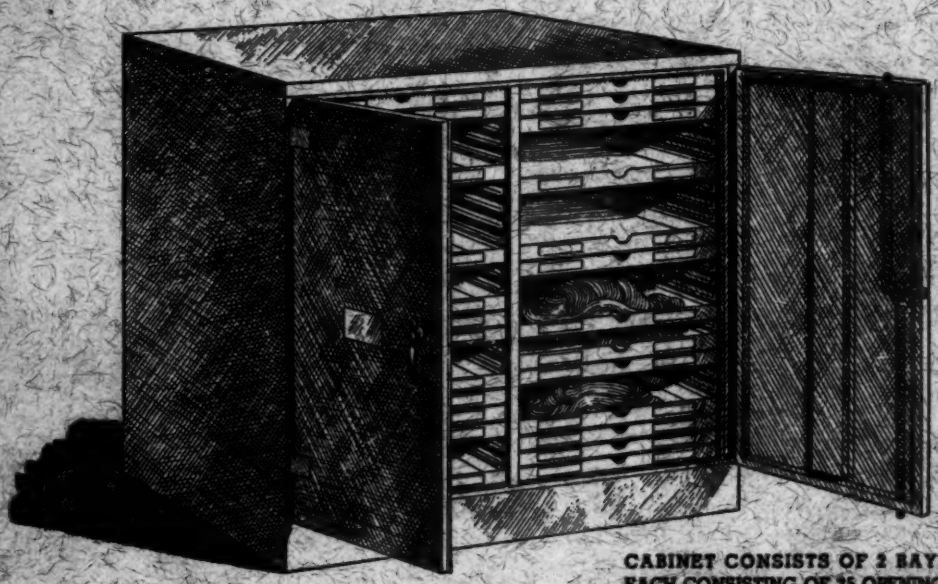
Secretary, H. R. Aldrich, New York, N. Y.

Treasurer, W. O. Hotchkiss, Scarsdale, N. Y.

Councillors

T. S. Lovering C. W. Knight Maurice Ewing	1946–1948
C. A. Anderson, Prescott, Ariz. Ernest Cloos, Baltimore, Md. M. King Hubbert, Houston, Tex.	1947–1949
G. M. Fowler, Joplin, Mo. F. J. Pettijohn, Chicago, Ill. Earl Ingerson, Washington, D.C.	1948–1950

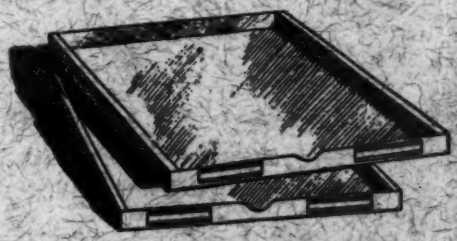
Welded Steel
PALEONTOLOGY *and* GEOLOGY CASES
with removable steel trays



CABINET CONSISTS OF 2 BAYS,
EACH CONSISTING OF 25 OPENINGS
FOR TRAYS—TOTAL 50 OPENINGS

NOW AVAILABLE—all steel cabinets and trays. Made of furniture steel, welded construction, with lock. Doors furnished with 3 point locking device.

VERMIN PROOF—MOISTURE PROOF



Green or Gray finish—Shipped set up ready for use

For complete information, write

W. B. WOOD COMPANY
CONTRACT DEPARTMENT
43 CLINTON STREET
NEWARK 2, NEW JERSEY, U.S.A.